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A new ergotaxonomy of the family Salamandridae Goldfuss, 1820 (Amphibia, Urodela)

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Several recent studies, particularly dealing with molecular phylogeny, have improved our knowledge of the relationships within the salamander family SALAMANDRIDAE. However, some only of these findings have resulted in formal taxonomic changes. In order to homogenize this taxonomy, we hereby recognize several new taxa at various ranks from subfamily to subspecies, and we propose a new comprehensive ergotaxonomy and nomenclature for the whole family. We also discuss some general questions of taxonomy and nomenclature, in particular regarding the concepts of species and genus, the use of taxonomic categories and nomenclatural ranks in taxonomy, the relationships between taxonomy and conservation biology, the various modes of definition of taxa (including diagnoses and cladognoses), the structure and length of scientific nomina, the status of online databases providing taxonomic and nomenclatural data, the designation of nucleospecies of nominal genera and the nomenclatural status of various nomina.

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"The whole of the Salamandridae require a thorough examination, in order that the relations of the different groups may be properly appreciated, and their characters fully established."

BELL, 1839: 134

"Ideally, all species that exist in each group should be recognized taxonomically. If biologists fail to detect undescribed species revealed by their studies, they are making one kind of error, and if they recognize more species than exist in nature, they are making a second kind of error."

HIGHTON, 2000: 215

"No names, no conservation."

PARRA et al., 2005: 45

TERMINOLOGICAL NOTE

In the present work, we strictly respect the rules of the *International Code of Zoological Nomenclature* (ANONYMOUS, 1999; "the *Code*" below), but we sometimes use different terminologies to designate the concepts of the *Code*, for reasons explained in detail by DUBOIS (2000, 2005*b*). We use the term *nomen* (plural *nomina*) for "scientific name" and the term *nominal-series* for the three "groups of names" recognized by the *Code*: *family-*, *genus-* and *species-series*. The use of the term "type" in nomenclature may be misleading (DUBOIS, 2005*b*), and this term is appropriately replaced by the term *onomatophore* (SIMPSON, 1940). There are different kinds of onomatophores. Those of family-series and genus-series nomina, termed respectively "type-genus" and "type-species" in the *Code*, are nominal taxa respectively of rank genus and species. They are designated below respectively by the terms *nucleogenus* and *nucleospecies* (DUBOIS, 2005*a-b*), which are not based on the root "type". Onomatophores of species-series nomina are *onymophoronts*, that can be designated as *holophoronts*,

symphoronts, *lectophoronts* and *neophoronts* (for “holotypes”, “syntypes”, “lectotypes” and “neotypes”). For the same reason, the term *monophory* (DUBOIS, 2005b) is here used instead of “monotypy” as used in the *Code*, and the term *onymotope* (DUBOIS, 2005b) instead of “type locality”. The term *neonym* (DUBOIS, 2000) is here used to designate the concept called “new replacement name”, “nomen substitutum” or “nomen novum” in various successive editions of the *Code*, and the term *archaenonym* (DUBOIS, 2005b) to designate the nomen replaced by a neonym. The term *anoplonym* (DUBOIS, 2000) designates a nomen that is not nomenclaturally available according to the *Code*; a frequently used subcategory of anoplonym is that of *gymnonym* (DUBOIS, 2000), a concept called “nomen nudum” in the *Code*. A distinction is made below between the formula *new combination*, in the strict sense of the *Code*, which involves a change in generic nomen, and the more general formula *new onymorph* (SMITH & PEREZ-HIGAREDA, 1986), which designates any different association of terms, with or without change in generic nomen, in a binomen or trinomen (see DUBOIS, 2000). Finally, DUBOIS (2006b) proposed to replace the *Code*’s term “nominotypical” by the term *hyponymous*: among two taxa hierarchically related and referred to the same series that bear the same nomen because of the Principle of Coordination, the term *epinym* designates the nomen of the superordinate taxon, and *hyponym* that of the subordinate taxon, both terms being *eponyms*. New nomenclatural acts implemented in this study or identified for the first time in previous works are pointed out below in bold characters: e.g., **new combination**, **new synonym**, **valid nucleospecies designation**.

INTRODUCTION

Taxonomy is a scientific discipline in permanent evolution, and will remain so for a long time still. This is mostly due to the importance of the *taxonomic impediment* (ANONYMOUS, 1994): only a small fraction of the earth’s biodiversity has already been collected and studied, and many pieces of information (on morphology, behaviour, genetics, phylogeny, distribution) about most “known” (i.e., named) taxa are still missing. For this reason, the classification of living organisms cannot be stable, and pleas for “taxonomic stability” amount in fact to apologies of ignorance (GAFFNEY, 1977, 1979; DOMINGUEZ & WHEELER 1997; DUBOIS, 1998a).

This is particularly true of the class AMPHIBIA, for which we are still far from having a complete or “subcomplete” list of the species still inhabiting our planet, many of which are threatened with extinction (STUART et al., 2008). The recent years have witnessed an unprecedented burst of works (1) describing new species and (2) proposing new hypotheses for the cladistic relationships between the known species, resulting in the recognition of new supra-specific taxa. It is likely that this trend will continue for several decades, and we are clearly in a very exciting period of the history of amphibian taxonomy.

The recent “*boost in species discoveries in a highly endangered vertebrate group*” (KÖHLER et al., 2005) has another important consequence. Strategies in global conservation policy devised on the basis of a highly incomplete or misleading taxonomy may prove inadequate, inefficient or even counter-productive (DUBOIS, 2003a). As pointed out by PARRA et al. (2005), development of a good taxonomy is a major requirement for the proper establishment of conservation priorities. This requires an intensification of field and laboratory work to collect and identify unknown species and for ascertaining species limits, recognition of so-called “cryptic” species or *dualspecies* (BERNARDI, 1980), and proper appraisal of *biodiversity hotspots* (see e.g. MEEGASKUMBURA et al., 2002) and of unique, isolated holophyletic groups, without close relatives in today’s fauna. These data are crucial for establishing taxonomic and geographic priorities in conservation strategies.

An important aspect of this question is that conservation actions are often facilitated, not to say made possible, by the existence of a *taxonomic and nomenclatural recognition* of the

units to be protected (species, subspecies): most legislative texts, red lists, custom documents, etc., only recognize such units if these bear Latin taxonomic nomina. The statement “*No names, no conservation*” (PARRA et al., 2005: 45) is warranted not only because identification of species (and other lower taxa) is necessary for proper appreciation of the conservation priorities, but also because it is often impossible to call for the legal protection of a “population” if it is unnamed taxonomically. This problem was well illustrated by a recent paper of MONTORI et al. (2008) about *Calotriton asper*, where the authors stated that, given the difficulties encountered for recognizing and naming taxa in this group, “*according to general conservation practices, none of the extremely differentiated populations of C. asper would be included in specific conservation plans*”, although “*loosing any differentiated population would imply the loss of the evolutionary process leading to that particular morphology*” (p. 48).

This is true not only at specific or infraspecific level, but also in higher taxonomy. It is important to recognize taxonomically holophyletic groups at various levels above species, even if they include a single or few species, or even perhaps more for this reason: thus, in salamanders, knowing that the genera *Protyphlobius*, *Dicamptodon* or *Hemidactylum* are the unique genera of their subfamilies or families currently alive (RAFFAËLLI, 2007) should call special attention of conservation biologists to these organisms.

Thus, to be fully efficient in conservation biology, any evolutionary, phylogenetic or taxonomic analysis of a population or group of populations that points to its uniqueness or distinctness must go to its end, i.e., to the formal taxonomic and nomenclatural recognition of this unit. Phylogenetic or other analyses uncovering new taxa that are not followed by their taxonomic recognition and naming amount to what BOCQUET (1976: 319) has called “*taxonomic cramps*”, which are in fact scientific errors, as highlighted by HIGHTON (2000, *liminar citation above*).

An additional, purely nomenclatural, problem is posed by the fact that, at low taxonomic levels, the nomenclatural transcription of trees of hypothesized relationships is made difficult by the arbitrary limitations imposed by the *Code* to the number of ranks that can be used in zoological nomenclature. Thus, in the genus-series of nomina, the *Code* only allows the recognition of two ranks, genus and subgenus. With the quick increase in the number of taxa that recent cladistic analyses often lead to recognize, this is clearly insufficient, and this explains the temptation of some to create additional ranks, not recognized by the *Code*, such as supergenus (e.g., RAFFAËLLI, 2007; VIETES et al., 2007) or series of successive ranks below subgenus and above species (e.g., HILLIS et al., 2001; HILLIS & WILCOX, 2005). Similarly, below the rank species, the *Code* only allows the use of two ranks, subspecies and “*aggregate of subspecies*”. It is clear that more ranks would be really necessary in zootaxonomy (DUBOIS, 2006a-c, 2007c), especially to express taxonomically fine cladistic relationships between species and phylogeographic relationships among populations of a species, and for use in conservation biology. However, until the *Code* is modified to allow for their recognition, the use of such ranks is not *Code*-compliant and should not be encouraged.

In the recent years, within the class AMPHIBIA De Blainville, 1816, some groups of the order URODELA Duméril 1806, and particularly in the family PLETHODONTIDAE Gray, 1850, have experienced important revisionary works and descriptions of new taxa (DUBOIS, 2005c; RAFFAËLLI, 2007). The family SALAMANDRIDAE Goldfuss, 1820 has been only moderately concerned by these changes. Several recently published studies, as well as our own experience

of these animals, suggest that the whole taxonomy of this family should be revised. In particular, the cladistic relationships hypothesized by WAKE & ÖZETI (1969) on the basis of morphological characters, that have been considered valid for several decades, were only partially confirmed by molecular data. A few changes have already been brought to this taxonomy recently, but they were partial, dealing only with some genera or groups of genera and leaving other taxa unmodified. This results in an unbalanced taxonomy which reflects only partially the recent increase in our knowledge of these salamanders. Our aim below is to propose a new *ergotaxonomy* (DUBOIS, 2005b) incorporating these new findings. This is certainly not the last word on this question, as the foreseeable discovery of new species, the re-evaluation of the status of some of the known species, and new cladistic data, based on both molecular and morphological analyses, will certainly be followed by other changes.

Finally, another important motivation for our proposals, similar to that of DUBOIS (1992) in the anuran family *RANIDAE*, is purely nomenclatural. It is to propose short and simple nomina for some taxa which will no doubt have to be recognized, sooner or later, by some authors in the future, and thus to avoid the publication for them of uselessly long, awkward and unpalatable nomina, which could not be modified by subsequent authors. Although this question is rarely tackled in scientific publications, we offer below a few general comments on the principles that should, in our opinion, guide the etymology, aspect, structure and length of zoological nomina.

TAXONOMIC METHODS AND CONCEPTS

TAXONOMY AND NOMENCLATURE

Although confused by some, taxonomy and nomenclature are two distinct fields. Taxonomy provides a classification of organisms into *taxa*, whereas nomenclature provides *nomina* to designate these taxa but does not deal with their establishment or definition. The existence of a universal nomenclature of living taxa regulated by international rules is a major social need as we need non-ambiguous designations for the same objects in all domains of activities, e.g., scientific publications, juridical texts, trade and custom documents, conservation biology, etc. This strong constraint implies that all these texts and documents follow the same nomenclatural system with a single nomenclatural hierarchy of taxa, in particular using similar binominal Latin nomina for "species". This does not mean that all taxa referred to this rank should be "equivalent" by some criterion: as a matter of fact, several different "kinds of species" need to be recognized in different situations. This has long been misunderstood, because of the frequent confusion made between the taxonomic concept of *taxonomic category* and the nomenclatural tool of *nomenclatural rank* (for more details, see DUBOIS, 2007a, 2008d). Here we make the distinction between these two concepts, which implies in particular that different taxonomic categories can be referred to the same nomenclatural rank.

Taxonomy consists in two rather different subfields that use largely different methods and concepts. The first one, the "science of species", was called *microtaxonomy* by MAYR & ASHLOCK (1980) and *eidonomy* by DUBOIS (2008b,d). Its duty is to define, recognize and describe taxa of nomenclatural rank *species*. These taxa can be hierarchically arranged in

more comprehensive taxa of higher ranks, and nowadays all authors agree that this arrangement should reflect somehow the phylogenetic relationships between organisms. This is the role of the second subfield of taxonomy, called *macrotaxonomy* by MAYR & ASHLOCK (1991) but that could better be designated as *phylonomy* (from the Greek *phulon*, in the sense of "kind, class", and *-nomos*, derived from *nemo*, in the sense of "I divide, I distribute"). This latter term is of more general meaning than that of *cladonomy* (BRUMMITT, 1997; DUBOIS, 1997, 2007a), which designates a particular conception of phylonomy that takes into account only the cladistic relationships between taxa, without caring for their age or their degree of divergence, a conception which is not shared by all taxonomists. This terminological difference is rooted in a traditional one in the literature on biological evolution that has been ignored in the recent years (MAYR & ASHLOCK, 1991: 206), the term *phylogenesis* (or *phylogeny*) being considered to apply to a combination of *cladogenesis* and *anagenesis* (sensu HUXLEY, 1957) (or *cladogeny* and *anageny*), whereas in many recent publications the terms *phylogeny* and *cladogeny* are considered synonyms, and the term *anageny* (and the concept to which it refers) ignored altogether.

We present below briefly the guidelines that we have followed here in our eidonomic and phylonomic decisions.

EIDONOMY: SPECIFIC AND INTRASPECIFIC CLASSIFICATION

Many theoretical discussions and publications have dealt with the "species concept". As discussed elsewhere in detail (DUBOIS, 2008b, 2009b), many of these discussions were obscured by the confusion made between different meanings of the term "species", in particular between its taxonomic and nomenclatural meanings. As a nomenclatural tool, *species* is a universal device allowing the allocation of any individual to a taxon of this rank, whatever philosophy of taxonomy is followed and whatever biological characteristics allow to define or recognize this taxon. In contrast, different taxonomic concepts of "species" have been and are used by taxonomists of different "schools" or to accommodate natural entities having widely different characteristics. These several distinct *taxonomic categories* or "specien" concepts, such as *mayron*, *simpson*, *klepton* or *klonon*, can be used for taxa at the *nomenclatural rank species* (DUBOIS, 1991, 2007a, 2008b,d, 2009b).

We here adopt a practical viewpoint that should in our opinion be used in salamandrids, as well as in most other zoological groups (DUBOIS, 2008b, 2009b). There exists a wide variety of evolutionary situations in nature, and, above all, a wide variety of information available to taxonomists. Requiring to apply a single, "unified", taxonomic species concept to all situations is possible only through using the "smallest common denominator" to all cases, i.e., through losing a lot of information which is sometimes available (and then useful), but sometimes not. This would be similar to taking advantage, for establishing the phylogeny and taxonomy of all vertebrates, only of the information available both for all fossil and recent known species, i.e., derived from the study of their skeleton. In contrast and in practice, to build their classifications, vertebrate taxonomists make use of all available characters, which are not as numerous and as varied in all cases.

Regarding the taxonomic species concept, the clearest situation is that of two entities occurring synchronically, sympatrically or parapatrically, and accessible to morphological,

genetic, molecular, karyological, behavioural and other studies. Such studies can allow to know whether a free bi-directional gene flow exists between the two entities, or whether this gene flow is absent, or restricted, unbalanced or uni-directional: whatever the reasons for this restriction in gene flow, such entities must be treated as species under a "biological" or "mixiological" taxonomic species concept (MAYR, 1942, 1963) or *mayron* (DUBOIS, 2007a), whereas entities connected by a free symmetrical gene flow must be considered conspecific, although possibly as different taxonomic subspecies. However, whenever two entities are allochronic or allopatric, or are not accessible to the studies mentioned above, this concept cannot be used and it is necessary to have recourse to "inference", through comparison with other "similar" pairs of entities, using for example "genetic distances", although the latter by themselves do not provide unambiguous information on the existence or potentiality of gene flow between two entities (DUBOIS, 1977, 1998a). In such cases, we are bound to use an "evolutionary" or "phylogenetic" taxonomic species concept or *simpson* (DUBOIS, 2007a), just like in paleontology we are bound to use only skeletal data for phylogenetic analysis and taxonomic decisions in the absence of other information. We used these concepts in our specific and subspecific taxonomy of the *SALAMANDRIDAE*. From a practical viewpoint, in several cases we tend to agree with HIGHTON (2000) in recognizing more species than in more traditional taxonomies.

In several amphibian groups, particular kinds of taxonomic species exist, for which the taxonomic categories of *zygoklepton* and *gynoklepton* can be used (DUBOIS, 1977, 1991, 2008b, 2009b; DUBOIS & GÜNTHER, 1982), but so far such kinds of entities have not been described in the *SALAMANDRIDAE*. In contrast, in this well-studied family, many taxa need to be recognized at ranks below species, not only for "pure" taxonomic reasons but sometimes for "practical" reasons related to conservation issues.

The recent development of the discipline of phylogeography (AVISE, 2000; ASSMANN & HABEL, 2009) provides important information for the understanding of historical and geographical relationships between populations of organisms. These data should be used as a basis for conservation decisions and actions, but this is made difficult by the frequent absence of a taxonomic and nomenclatural transcription of these findings. This may result from the limitations mentioned above put by the *Code* on the nomination of infraspecific taxa, but also from the fact that many researchers in phylogeography do not come from the discipline of taxonomy and lack a proper taxonomic "culture". Thus, instead of using the two infraspecific ranks recognized by the *Code*, they coined their own concepts and terms, such as those of "evolutionary significant unit" (ESU) or of "conservation management unit" (RYDER, 1986; MORITZ, 1994; FRASER & BERNETCHEZ, 2001). However, as these units do not correspond to formal taxonomic units bearing Latin nomina, they cannot easily be used for the protection of endangered taxa or their habitats, at least with the tools provided by the laws or regulations based on official texts or lists using such nomina. We think "phylogeographers" should also become "phylogeotaxonomists" and provide Latin nomina based on the rules of the *Code* for the units they recognize. This does not require to abandon the specific units such as ESU, but to distinguish the fact that these units designate *taxonomic categories* from the existence of formal units which correspond to standard *nomenclatural ranks*. In other words, a unit may well be defined *both* as an ESU from an evolutionary point of view and as a subspecies or an exerge (see below) from a nomenclatural point of view. The present paper provides such examples. Of course, to name taxa validly under the rules of the *Code*, taxonomists are bound

to follow the latter and also its limitations in the number of ranks that can be used below species, arbitrarily limited to two, but hopefully modifications will be brought to this text to abandon these limitations (see DUBOIS, 2006b).

The *Code* provides the possibility to recognize and formally name taxa at a rank intermediate between species and subspecies. By similarity with the situation in other nominal-series (where the first rank below a primary rank starts by sub-: subclass, suborder, subfamily, subtribe, subgenus), it would be more logical to use the rank subspecies immediately below the rank species, and then infraspecies below (DUBOIS, 2006a), but to respect the *Code* we here interpolate one rank between species and subspecies. For taxa at this rank, rather than the unpalatable formula "aggregate of subspecies", we use VERITY's (1925) term *exerge*, as proposed and explained by BERNARDI (1980).

PHYLONOMY: SUPRASPECIFIC CLASSIFICATION

The numerous cladistic studies, mostly based on nucleic acid sequencing, that have been carried out in the recent years, often suggest rather detailed cladistic relationships between species, which can be expressed taxonomically and nomenclaturally through hierarchies, as discussed in detail by DUBOIS (2007a, 2008d). However, this transcription of cladistic hypotheses into classifications poses two kinds of problems, taxonomic and nomenclatural.

From a taxonomic point of view, most authors nowadays agree that only should be recognized taxa that appear, at a given stage of research, to correspond to "monophyletic" (sensu HENNIG, 1950) or better *holophyletic* (ASHLOCK, 1971) groups. This does not mean that all hypothesized holophyletic groups, i.e., all nodes in the trees, should be taxonomically recognized, for two distinct reasons.

The first one is that, even if we had a complete inventory of the animal species of the earth, and a completely resolved tree of relationships between them, it would not be appropriate to name all nodes, because this would result in very cumbersome and useless taxonomies that would be as uninformative as mere chaos. As a matter of fact, depending on the structure of the tree, up to $(n - 1)$ supraspecific taxa might be required to express taxonomically the cladistic relationships between all n species of the inventory (SZALAY, 1977: 363; DUPUIS, 1979: 45; DUBOIS, 2005b: 393).

The second problem results from the uncertainty of many of our results, which makes many of our trees labile. In most zoological groups, successive cladistic analyses provide different results, for various reasons (problems in vouchers' identification; different samplings of species and characters; different morphological or molecular methods; different algorithms for tree construction and for testing tree robustness and reliability). This does not mean that we should not use these successive hypotheses as temporary bases for the building of successive "working taxonomies" or *ergotaxonomies* (DUBOIS, 2005b), but that we should be aware of their temporary nature.

In this respect, it is useful to make the distinction between two kinds of information provided by cladograms. One is the recognition of rather small holophyletic clusters of closely related species, and the other is the respective and hierarchical relationships between these clusters. In well-studied zoological groups, after a certain time, a rather high robustness exists

regarding the first kind of information, but this robustness may be much longer and difficult to obtain for the cladistic relationships between these clusters. Thus, several cladistic analyses of a zoological group (e.g., a family) composed of twelve species 1 to 12 may all agree in recognizing six specific clusters, A (1 + 2), B (3 + 4), C (5 + 6), D (7 + 8), E (9 + 10) and F (11 + 12), but disagree regarding the relationships between these clusters. Let us imagine for example that four successive analyses of this group provide the following results, $(A(B(C(D + (E + F))))), (C(B(A(D + (E + F))))), (C(A + B)(D + (E + F)))$ and $((B(A + C))(D + (E + F)))$. A prudent, conservative and probably robust taxonomic transcription of these results would be: (1) to recognize A, B, C, D, E and F as taxa (e.g., genera); (2) to recognize (E + F), which comes back in all analyses, as a taxon G (e.g., a tribe); (3) in order to respect the hierarchical taxo-nomenclatural structure (see DUBOIS, 2008d), to recognize another tribe H for its sister-group, i.e., the genus D; (4) to recognize (G + H), which comes back in all analyses, as a taxon I (e.g., a subfamily), (5) to recognize three additional subfamilies, J, K and L, respectively for the genera A, B and C. This is because the mutual relationships between A, B, C and I are not yet clarified, which does not allow a robust taxonomic statement in the form of a hierarchy between them. This amounts to recognizing taxonomically all the robust specific clusters, but some only of the nodes of the trees obtained, those that appear constant in all analyses. In such taxonomies, taxa which are considered sister-taxa or members of an unresolved polytomy are *parordmate* (DUBOIS, 2006b) and must be given the same nomenclatural rank, which is just below that of their common *superordmate* taxon and just above that of their *subordmate* taxa if they exist (DUBOIS, 2008d).

Ranks as used in such hierarchies have a single purpose: that of providing unambiguous information on the *structure of the tree* used as a basis for the taxonomy, i.e., on sister-taxa and more remote relationships between taxa. They do not provide information of any kind, be it biological or historical (age), on the taxa referred to any particular rank. In other words, a family of bats and a family of bees are by no criterion *equivalent* (DUBOIS, 2007a, 2008d). However, this arbitrariness of ranks does not mean that allocation of ranks to taxa should be made blindly and without reflection. Three main constraints should be considered in this respect. The first one is that a few major "primary key ranks" should be considered universal and compulsory in all ergotaxonomies (DUBOIS, 2006a, 2007a, 2008d; KUNTNER & AGNARSSON, 2006) regnum, phylum, classis, ordo, familia, genus and species. All zoological organisms should be referable to taxa at these seven ranks, for simple reasons of indexation of the taxonomic information, and even if this entails a certain "taxonomic redundancy" in some cases (DUBOIS, 2007a, 2008d). The second constraint is that "major", i.e., "well-known" taxa, should be ascribed primary key ranks (such as order or family) and not secondary key ranks (such as legio or phalanx) or subsidiary ranks (such as suborder or subfamily) (for more details, see DUBOIS, 2006a). The third constraint is that particular attention should be given to the rank genus, because this rank plays a very special role in zoological nomenclature, being part of the binomen that designates each species. It is not enough to say that, to be recognized as a genus, a group should be "holophyletic" or should correspond to a "lineage" or a "clade" (for a criticism of the use of these terms, see DUBOIS, 2007a, 2008d), because knowing that a group includes all the descendants of an ancestral species does not in the least tell us whether this "clade" should be considered a genus, a tribe, a subgenus, a species-group or something else. We need additional criteria, which are not purely cladistic, but which take other information into account.

This matter was discussed at length by DUBOIS (1988*b*, 2004*b*), who suggested a series of criteria, including a mixiological one (see below), for the delimitation of genera. FROST et al. (2006) failed to discuss these criteria and did not provide any explanation on the criteria that they used to decide to recognize a "clade" either as a genus, a subgenus, a species-group, a tribe, a subfamily, a family or whatsoever. As a result, their generic taxonomy is highly unbalanced and poorly informative, as in some cases they grouped in the same genus several widely divergent "clades", whereas in other cases with similar species richness and diversity they adopted a much more divided generic taxonomy, presumably to respect "tradition" and "consensus". An immediate consequence of such a "methodology" is that this taxonomy fails to provide morphological diagnoses for many of the genera. We think the choice of the "level" where phylogenetic trees should be "cut" to insert the rank genus is an important matter because it has considerable consequences on the way eidonomy progresses. This choice should not be based on cladistic data alone (as a "clade" is a "clade", whatever its age, specific richness and diversity) but on other, non-cladistic criteria. Many field naturalists and taxonomists, when they observe or collect animals in the field, will try to identify them using monographs, revisions, keys, which very often are based on taxa of rank genus. Genera that include very divergent subgroups (e.g., the genus *Rana* as understood in many traditional works e.g., INGER, 1954, 1966; TAYLOR, 1962) cannot be properly diagnosed morphologically and do not guide taxonomists for the recognition of new species, leading often to improper comparisons and taxonomic decisions. Given the present situation of taxonomy, where many new species await discovery, recognition and description before getting eventually extinct, using such "vague" genera is not doing a service to the study of biodiversity. We think zootaxonomists should only use genera that can be clearly defined by morphological diagnoses, usable by all field naturalists and zoologists.

Below, we afford the rank genus to well-defined and cladistically supported *holophyletic* groups of closely related species that share a number of characters (both apomorphies and plesiomorphies) providing morphological, but also sometimes behavioural and ecological, diagnoses. These species therefore share not only a general morphology but also a general "ecological niche" (INGER, 1958; DUBOIS, 1988*b*) and they are usually separated, according to these criteria, by a "gap" from the species of the closely related genera (MAYR, 1969; DUBOIS, 1988*b*). Within these groups, it is sometimes possible to recognize holophyletic subgroups that are not as strongly divergent and that may overlap in some characters, being often more difficult to diagnose morphologically or ethologically, and among which hybridization may remain possible. We think these groups should also be recognized as taxa, but at ranks lower than genus.

NOMENCLATURE RANKS

In this paper we follow a nomenclature that fully respects the rules of the *Code*, particularly regarding the nomenclatural ranks allowed by this text. The *Code*, although it lists only five "standard" family-series ranks (superfamily, family, subfamily, tribe and subtribe), does not preclude the possibility to use further lower family-series ranks, as it accepts "*any other rank below superfamily and above genus that may be desired*" (Art. 35.1). We use this opportunity to recognize, below these five standard ranks, taxa at the rank infratribe,

with the ending *n.a.*, as suggested by DUBOIS (2006a: 211). However, for supraspecific taxa below the rank genus, the *Code* only allows the use of two ranks, subgenus and “aggregate of species”. Therefore, we refrained here from using ranks such as supergenus, infragenus or hypogenus, although we regret this impossibility (see DUBOIS, 2006a)

Below the rank genus, in agreement with other recent works in the URODÉLIA (e.g. PARRA-OLEA et al., 2004; McCRAVIE et al., 2008), we prefer to recognize first subgenera rather than “species-groups” or “species-complexes”, as it is easier to designate a taxon by a single nomen than by a long expression using several terms, as shown by comparing the two sentences: (1) “In all species of *Pyronota*, the dorsal colour is usually green with spots”; (2) “In all species of the *Triturus marmoratus* species-complex, the dorsal colour is usually green with spots”. This is, in fact, the primary function of having a zoological nomenclature, rather than simply diagnoses, definitions or descriptions, or than numbers, codes or other non-verbal systems. Whereas computers use such coded systems, we, as humans, rather use words to designate things or concepts. Unfortunately, for additional subdivisions in the genus-series below the rank subgenus, taxonomists are bound to use such cumbersome designations (e.g., “*Triturus vulgaris* supraspecies”), because of the current limitations imposed by the *Code*. Anyway, the nomina of “intermediate” taxa such as subgenus or supraspecies do not need to be written every time a taxon is mentioned in the text. It may be useful to write the complete nomen of a taxon, with these nomina between parentheses, at the first mention of a taxon in a publication, or in a table like table 5 below, but then, in the text, a species needs only be mentioned by its binomen and a subspecies by its trinomen, without writing all these additional nomina (see below). In a non-taxonomic publication dealing with these taxa, the nomina at these intermediate ranks do not even need to be mentioned once.

Below the rank subgenus and above the rank species, the *Code* (Art. 6.2) offers the possibility to formally recognize taxa of a single rank, “aggregate of species”. Their nomina, which belong in the nomenclatural species-series, may be interpolated between the genus-series nomen or nomina and the specific nomen, and the Principle of Priority applies to such nomina. To designate such taxa, rather than using multi-word formulae like “aggregate of species”, “species-group” or “species-complex”, the term *supraspecies* is available (GRINBERG & LAMOTTE, 1980; DUBOIS, 2006a) and is used here.

In a nomenclatural hierarchy as described above, four different situations can be distinguished regarding the number of subordinate taxa for each taxon. These situations can be described as four *categories of hypotaxy* (from the Greek *hypotaxis*, “dependence, submission, subordination”). As they correspond to different topologies of trees, with or without polytomies, they partly reflect the resolution of the tree and they can inform us about it.

(1) A given taxon may include only *one* immediately subordinate taxon, a situation which may be called *monohypotaxy* (from the Greek *monos*, “single, unique” and *hypotaxis*, “subordination”) ¹. In such a case, the two successive ranks are clearly *redundant*, which means that

¹ The term *monotypy* is sometimes used in the taxonomic literature to designate a taxon that includes a single subordinate taxon or no subordinate taxon at all; thus the term *monotypy* is sometimes applied to designate a genus with a single species or a species that does not include subspecies. With this meaning the term *monotypy* refers to a taxonomic concept. But this term is confusing as it is used in the *Code* in a different sense, to designate a nomenclatural concept (i.e., mode of designation of onomata) for a formal taxon, either in the genus-series (Art. 68.3 and 69.3) or in the species-series (Art. 73.2). This confusion is illustrated for example by stating that a monotypic species (i.e. without subspecies) can well bear a nomen that relies on a

they do not provide distinct *taxonomic* information - but they may be useful for mere *nomenclatural* reasons (for more details, see DUBOIS, 2007a, 2008d).

(2) A given taxon may include *two* parordinate taxa of just lower rank, a situation which may be called *diphypotaxy* (from the Greek *diploos*, "double" and *hypotaxis*, "subordination"). Taxonomically, this can be interpreted as meaning that a simple hypothesis of relationships between these two taxa exists, these two parordinate taxa can be considered as sister-taxa. Although this interpretation can be challenged by subsequent works, as long as it is not such a taxonomy appears like a "final" one.

(3) A situation of *polyhypotaxy* (from the Greek *polus*, "numerous" and *hypotaxis*, "subordination") occurs whenever *more than two* parordinate taxa are subordinate to a just superordinate taxon. The taxonomic meaning of this situation is unclear, as two different cases may account for it: (a) these parordinate taxa are the members of a still unresolved polytomy, which subsequent work can possibly help to solve, (b) an hypothesis already exists regarding the relationships between the members of the polytomy, but it was not implemented into the ergotaxonomy in order to limit the number of ranks of this taxonomy.

(4) Finally, a taxon may include *no* subordinate taxon, being the "terminal" lower taxon in a nomenclatural hierarchy. This situation which may be described as *anhypotaxy* (from the Greek *aneu*, "without" and *hypotaxis*, "subordination"). Given the current nomenclatural rules of the *Code*, this can occur only in two cases, when the "final" taxon is either a species or a subspecies². By definition, all nomina at ranks above the rank species designate taxa that include at least one species, even possibly still unnamed and undescribed, so they cannot fall in the category of anhypotaxy.

Whereas mono-, diplo- and anhypotaxy are expected to be observed in a well resolved tree and taxonomy, polyhypotaxy may reflect partial irresolution of a tree. Therefore, an ergotaxonomy with a high rate of polyhypotaxy is unsatisfactory and clearly requires further work. This does not mean however that an ergotaxonomy without polyhypotaxy would be definitive and perfect, as inclusion of new taxa and new data may lead to change it.

Because of the nomenclatural parsimony resulting from the Principle of Coordination (see DUBOIS, 2008d), less nomina than taxa are necessary to express a hierarchical taxonomy, especially at higher ranks because more ranks can be recognized in the family-series than in the other nominal-series. This can be measured by a *nomenclatural parsimony ratio*, NPR = number of distinct nomina / number of taxa. The terms "distinct nomina" mean that the different avatars of a nomen that may exist at different ranks within a nominal-series (e.g., family and its hyponymous subfamily, genus and its hyponymous subgenus, etc.), are different *morphonyms* but are the same *nomen*, with the same onomatophore, author and date (DUBOIS, 2000). The ratio NPR is lower when nomenclatural parsimony is higher. The more a taxonomy is balanced and resolved, and the lowest its rate of polyptaxy, the lowest its NPR is.

holophoront fixed by original designation, or on symphoronts among which not lectophoront was ever designated, i.e., two situations that do not correspond to "monotypy" in the sense of the *Code*. This confusion is avoided by using the terms *innehypotaxis* and *anhypotaxis* for the taxonomic concepts, and *monophory* (DUBOIS, 2005b) for the nomenclatural concept. The existence of this confusion, that has been corrected until now in all the literature, is an additional reason for rejecting the use of the term "type" and terms based on this root in taxonomy and nomenclature, beside those given by DUBOIS (2005b).

² This is another situation for the use of the traditional, but misleading term *monotypy*: see intrapagina note above.

THE USE OF HYBRIDIZATION DATA IN TAXONOMY

Hybridization experiments, which were very “fashionable” in the first half of the 20th century and until the seventies, have stopped being so in our “all-cladistic” age, but it is to be hoped that future taxonomists will again get interested in such data, as they are very rich in information for the understanding of the evolution of zoological groups (see DUBOIS, 1988b). This particularly applies to works on the family SALAMANDRIDAE, in which for several decades these data have been considered of utmost importance for establishing taxonomic groups (e.g., in the genus *Triturus* as traditionally understood), but largely ignored in the recent years.

Hybridization data can be useful at two different levels in taxonomy, in eidonomy for the recognition of taxonomic species and in phylonomy for the recognition of taxonomic genera.

A few recent authors proposed a concept of taxonomic species as a “lineage”, according to which, as soon as two groups of individuals are liable to produce together fertile hybrids, they should be referred to the same species “in spite of appearances, when two interbreeding organisms taken in apparently diverging lineages leave fertile offspring, there is no reason to conclude the existence of distinct species. If this indeed occurs, no new branch has appeared in the phylogenetic tree. Whatever the definition of species may be, considering ‘interpecific hybridization’ is conceptually inconsistent.” (SAMADI & BARBEROUSSE, 2006: 515-516). We fully and strongly disagree with such a statement, which is at complete variance with the use of the category species in most zootaxonomic publications until now. To drastically “redefine” nowadays the “species concept” along such guidelines would introduce extreme confusion and chaos in the discussion on these matters which is already very complex, and is certainly not to be recommended! If these idea had to be followed, then almost all ducks in the world (family ANATIDAE), which hybridize freely in captivity but rarely in nature, would belong in a single taxonomic species, and the same would be true in innumerable other cases over the whole of zoology (see DUBOIS, 1988b).

As a matter of fact, the concept envisioned by these authors is not that of “species”, at least as has been understood by the overwhelming majority of authors for two centuries (i.e., a set of individuals which *in nature* breed *freely* together), but another concept, designating all the individuals susceptible of producing together, even in artificial conditions, viable hybrids. This concept was called *coenospecies* by TURESSON (1929) and *syngameon* by CUÉNOT & TÉTRY (1951: 455) (see BLIGNARDI 1980: 396, 398). This is indeed a useful concept, but not for the taxonomic category of species. It was called upon (DUBOIS, 1982, 1988b) to help defining a particular taxonomic category of rank genus or “genion” (DUBOIS, 2007a, 2008d, 2009b). The term *coenospecies* being misleading (suggesting that it is a “kind of species”) and *syngameon* being preoccupied by an homonymous term designating another category (LOTSY, 1918), this taxonomic concept can be known as *coenogemon* (DUBOIS, 2007a) or *coenogenus*, better *mixogemon* or *mixogenus* (from the Greek *mixis*, “mixing, sexual intercourse” and *genos*, “descent, race, family”).

Contrary to what some believe, crossability between species is not a *character* of each of these species but a “relational taxonomic criterion” (DUBOIS, 1988b) or *relaxter* between them (DUBOIS, 2004b). Its use does not rely on its bearing information on cladistic relationships, but on its measure of the overall genetic divergence between the genomes of two species after their

separation. The ability of two half-genomes to build together a hybrid adult organism through the very complex processes of ontogeny cannot be due to convergence or chance, but to the conservation of common or very similar *mechanisms of genetic regulation*, and this is a much more sensible and meaningful measurement of "genetic distance" between them than any index based on *structural similarity of genomes* (DUBOIS, 1988b).

A mixogenus is a taxon of nomenclatural rank *genus* that includes at least *some* taxonomic species among which adult diploid true hybrids (not polyploid, gynogenetic or androgenetic offspring) are known to have been produced, either in natural or in artificial conditions, between specimens belonging to two distinct taxa, although in nature the latter behave as normal species (e.g., mayrsons or kleptons). This does not mean that *all* species included in a mixogenus should be hybridizable, because of the characteristics of interspecific hybridization in animals, in particular its asymmetry, non-transitivity and quick disappearance between sympatric species (for details, see DUBOIS, 1988b), but that any other species subsequently discovered to have successfully crossed with a member of the mixogenus (and also in some cases other related species) should be included in the latter. Such a taxonomic concept is fully compatible with the requirement that, to be recognized as a taxon of nomenclatural rank *genus*, a group should be holophyletic. It just provides an additional criterion for placing the "bar" where to insert the "genus level" among various hierarchically related "clades". DUBOIS (2004b) provided detailed explanations and recommendations in this respect. It should be stressed that, to be usable, the cross should have resulted in *adult* diploid true hybrids, but that the latter may be fertile or sterile, for reasons explained in full detail by DUBOIS (1988b).

The use of hybridization data at the "species level" is different, as briefly tackled above. Many cases are known of "good species" that rarely, occasionally or even regularly hybridize in nature without having to be considered "conspecific". Mayrsons connected in nature by "hybrid zones", like *Bombina bombina* and *Bombina variegata*, are not rare in amphibians. The important point here is the structure and dynamics of the hybrid zone. Very schematically, if in the latter a bidirectional gene flow exists between the two entities, with symmetric bilateral genetic introgression that tends to homogenize both gene pools as a single one, they belong in the same mayron (possibly as two distinct submayrsons). In contrast, if this zone acts as a (possibly leaky) barrier between both taxa, allowing them to remain clearly distinct and "recognizable" (morphologically, molecularly or both), they should be considered distinct mayrsons (DUBOIS, 1977, 1998a).

We used these guidelines to support some of the taxonomic changes presented below. Many cases of hybridization, whether natural or artificial, have been documented in the *Salamandridae* in the last century. Regarding the crossability criterion at the nomenclatural level of *genus*, the requirement imposed by the use of the mixogenus taxonomic category is that no adult hybrid (whether fertile or infertile) be known to have been produced between two species referred to different taxonomic genera. This clearly applies to most known cases of successful interspecific hybridization in this family, which occurred between taxa referred below to the same genus. Two problematic cases, between the genera *Pleurodeles* and *Typhlotriton* on one hand, and among the modern European newts on the other, are discussed in more detail below. At the specific level, a number of subspecies recognized below are known to be connected by hybrid zones which seem to allow free bidirectional gene flow between

them. In several other cases, hybrids are known to exist, or to have existed, in nature between two entities, but the available data do not suggest that a free symmetric gene flow exists between them, and we recognize them as distinct species. This is the case in particular in several groups of modern European newts, as briefly discussed below

TAXOGNOSES

Whereas nomina of taxa are not "defined" but "attached" to taxa through their onomatophores (DUBOIS & ÖHLER, 1997, DUBOIS, 2005b, 2007a, 2008d), taxa are indeed "defined" (not "discovered", as stated by some, because taxa are concepts, not objects). There are several ways of "defining" the taxa as recognized by a taxonomy. Most of them belong in two major categories: (1) "phenetic definitions" such as the "diagnoses" traditionally used in taxonomy, and (2) "phylogenetic definitions" (DE QUEIROZ & GAUTHIER, 1990, 1994). These different kinds of definitions do not play the same role or give the same information and it is useful to provide several of them altogether when defining a taxon (see e.g. the example in DUBOIS, 2007a Appendix). This is what we do below, so we here define the terms we use.

We use the new term *taxognosis* (from the Greek *taxis*, "putting in order" and *gignosko*, "I know") as a general term for any *definition of a taxon*. Taxognoses are of two main sorts: (1) a *physiognosis* (from the Greek *physis*, "nature, inborn quality" and *gignosko*, "I know") is a taxognosis that provides *characters* considered to allow a non ambiguous identification of the taxon, irrespective of any cladistic hypothesis; (2) a *cladognosis* (DUBOIS, 2007a, from the Greek *klados*, "branch" and *gignosko*, "I know") is a "phylogenetic definition" of the taxon, i.e., a taxognosis that is associated with a cladistic hypothesis. Both these categories contain subcategories.

(1a) A *diagnosis* (traditional term in taxonomy, from the Greek *diagnosis*, "distinction, discrimination") is a physiognosis based on "character states" or *signifiers* (ASHLOCK, 1985) that are considered to be differential for the taxon, i.e., shared by all members of the taxon and absent in all non-members

(1b) An *idiognosis* (from the Greek *idios*, "one's own, particular, proper" and *gignosko*, "I know") is a physiognosis based on signifiers that are considered to provide a brief description or characterisation of a taxon, including both diagnostic (differential) signifiers and signifiers shared with other taxa.

(2a) An *apognosis* (DUBOIS, 1997, from the Greek *apo*, "from, away from" and *gignosko*, "I know") is a cladognosis based on signifiers that are considered to be shared by all members of the taxon and absent in all non-members, and that are considered, on the basis of a cladistic analysis and hypothesis, to be autapomorphic for the taxon. Such cladognoses have also received the long and cumbersome designation of "apomorphy-based definitions" (DE QUEIROZ & GAUTHIER, 1990)

(2b) A *coinognosis* (DUBOIS, 2008d; from the Greek *koinos*, "common, kindred", and *gignosko*, "I know") is a cladognosis based directly on the hypothesized cladistic relationships between taxa. Such cladognoses, which received no designation by DE QUEIROZ & GAUTHIER (1990) and their followers, are of four kinds. Two of them, first defined by DE QUEIROZ

& GAUTHIER (1990), are based on explicit formulations of *hypotheses of cladistic relationships* between organisms or taxa, and on statements about “common ancestors”

(2ba) A “node-based definition” (DE QUEIROZ & GAUTHIER, 1990), or more briefly a *rhizognosis* (DUBOIS, 2008*d*; from the Greek *rhiza*, “root”, and *gignosko*, “I know”), is a coinognosis defining a taxon as including all organisms or taxa stemming from the most common ancestor of two specified organisms or taxa.

(2bb) A “branch-based definition” (DE QUEIROZ & GAUTHIER, 1990), or more shortly a *caulognosis* (DUBOIS, 2008*d*, from the Greek *kaulos*, “stalk”, and *gignosko*, “I know”), is a coinognosis defining a taxon as including all organisms or taxa sharing a more recent common ancestor than with another taxon.

As a matter of fact, statements about “common ancestors” (which in most cases are unknown and hypothetical) are not indispensable to provide non-ambiguous definitions of taxa, at least within the frame of a given cladistic hypothesis and ergotaxonomy. Both these later definitions can be reformulated sparing the *designation* of these unknown ancestors, by using the concept of monophyly *sensu* HENNIG (1950) or holophyly (ASHLOCK, 1971): a holophyletic taxon includes an ancestor and all its descendants. Such coinognoses are based only on the *inclusion* of organisms or taxa in the taxon, sometimes combined with the *exclusion* of other organisms or taxa, without explicit statements about the ancestors. As it relies on the concept of holophyly, it makes sense only when applied to a given cladistic hypothesis. These two kinds of coinognoses, used e.g. in DUBOIS (2006*a*, 2007*a*: Appendix) have remained until now unnamed.

(2bc) An “inclusion-based definition” or more shortly an *entognosis* (from the Greek *entos*, “within, inside” and *gignosko*, “I know”), is a coinognosis defining a taxon as the *least inclusive holophyletic* taxon (i.e., based on a cladistic hypothesis) *including* one or several organisms or taxa. The mention of “least inclusive” is important here, as without this mention the coinognosis would apply to the whole animal kingdom, not to say the whole tree of life. Although formulated differently, in practice an entognosis is strictly equivalent to the rhizognosis based on the same included organisms or taxa.

(2bd) A “bidirectional-based definition” or more shortly an *entexognosis* (from the Greek *entos*, “within, inside”, *exo*, “outside”, and *gignosko*, “I know”), is a coinognosis defining a taxon as the *most inclusive holophyletic* taxon (i.e., based on a cladistic hypothesis) *including* one or several organisms or taxa and *excluding* one or several other organisms or taxa. Although formulated differently, in practice an entexognosis is strictly equivalent to the caulognosis based on the same included and excluded organisms or taxa.

Such definitions are used in fact for the allocation of nomina to taxa within the frame of nomenclatural rules. Entexognoses apply to the situation of allocation of nomina to taxa of the three lower nominal-series recognized by the *Code*, which rely on onomatophores only (combined with the Principle of Coordination). They also correspond to the situation, described in the rules proposed by DUBOIS (2006*a*) for class-series nomenclature, of choronyms, i.e., nomina that apply to orotaxa, being based both on onomatophores and onomatostases. In contrast, in these rules, entognoses correspond to the situation of nesonyms, that apply to metrotaxa and are based on onomatophores alone (but without a Principle of Coordination). This rather complex point is not developed further here as it is beyond the

scope of the present work (see DUBOIS, 2007a, 2008d). The cladognoses of taxa given in DUBOIS (2007a: Appendix) are entexognoses.

In the present work, for each taxon erected or "resurrected", we provide three different taxognoses: an entexognosis, a diagnosis (in a table) and an idiognosis.

COMMENTS ON NOMENCLATURE

ZOOLOGICAL NOMINA SHOULD BE SHORT AND SIMPLE

Many recently published cladistic analyses imply taxonomic changes. When carried to their logical conclusion, new cladistic hypotheses, derived from such analyses, lead to new supraspecific classifications, and often require the creation of new nomina for newly defined taxa. The *Code* only provides a few rules and recommendations for the mode of formation of zoological nomina, and these rules are not very binding. As far as the *Code* is concerned, taxonomists are basically "free" to coin every nomina they like. Does this almost complete "freedom" mean that they should not follow any guidelines in this respect?

As a matter of fact, in the recent years, as well exemplified in the AMPHIBIA, this "freedom" has resulted in a clear trend to create long, unpalatable nomina. Such nomina are often created on the basis of complex etymologies, derived from Latin, Greek or modern terms or roots combined together. Such long and complex nomina may appear to some more "serious" or "scientific" than short and simple ones, but they are not necessary. The *Code* does not in the least require the use of complete roots or "correct etymologies" for scientific nomina – which would be very difficult indeed as there are not and cannot be rules for a "correct" derivation of a nomen from a Latin or Greek etymology, or, even worse, for a "correct latinisation" of non-Latin terms (for more details, see DUBOIS, 2007b).

The *Code* does not either "forbid" the creation of long nomina. In its Appendix B, it simply "recommends" that nomina "should be euphonic and easily memorable and should not be liable to confusion with those of other taxa of any rank or with vernacular words". The criterion of "euphony" is of difficult application, as the same term may sound more or less "euphonic" according to the culture or language spoken by a person. However, it seems clear that a brief nomen composed of simple syllables with only two or three letters each (one or two consonants and a single vowel) will be considered "simple and euphonic" by all, whereas more complex structures may not. Despite the absence of rule in this respect in the *Code*, NG (1994) aptly criticized the creation of very long nomina, and gave some extreme examples, such as the generic nomen *Siemienkiewiczzechuogammarus* Dybowski, 1926 (14 syllables, 29 letters) and others, that were invalidated by the International Commission on Zoological Nomenclature (ICZN) for being a potential cause of "greater confusion than uniformity" (ANONYMOUS, 1929: 1). Beside the length proper, i.e. the number of letters, a nomen may be characterized by its phonetic complexity, i.e. its number of syllables or vowels. This is so because in classical Latin all vowels were pronounced separately (like in modern Spanish or Turkish), so that a nomen like *Hyalmbatrachium*, which contains 8 vowels, must be considered to consist in 8 different syllables (*Hya-lm-ba-trach-i-um*).

When coining new nomina, many zoologists seem to forget the basic purpose of these terms. Scientific nomina are not descriptions, diagnoses, statements on the characters, distribution or other characterisations of the taxa they designate. They are not models, evolutionary, phylogenetic or genetic theories about the hypothesized origin of these taxa. They are not praises for their authors (see DU BOIS, 2008a), for the discoverers of the taxa or for the persons to whom they may be dedicated. They are just neutral labels meant at designating *unambiguously* and *universally* a given taxon *within the frame of a given taxonomy*, i.e., allowing the automatic pointing to the taxa recognized by taxonomists at a given stage of their research. These labels allow storage and retrieval of the information accumulated in taxonomies (MAYR, 1969), but they are not meant at expressing this information by themselves. As such, nomina are fully *meaningless* and should remain so. This is why the *Code* expressly states that availability of nomina “*is not affected by inappropriateness*” (Art. 18), and allows a new generic or specific nomen to be “empty of meaning”, for example for being “*an arbitrary combination of letters provided this is formed to be used as a word*” (Art. 11.3).

Famous examples of “empty nomina” include the crustacean generic nomina *Anilocra*, *Canolua*, *Carolana*, *Conilera*, *Nelocira*, *Nerocila*, *Olenocira* and *Roemela*, all created by LEACH (1818: 347-351) as anagrams of the surname “Carolina” or “Caroline”. they are all short, euphonious, and fully appropriate for zoological genera. The same system could appropriately have been or be followed in many other genera. Thus, if the genus amphibian genus *Bufo* had to be dismantled (a debated question not discussed here), why not use for the new taxa anagrams of this nomen, like “Bofu”, “Fobu” or “Fubo”, or similar but slightly different nomina like “Bufa”, “Bufus” or “Fufo” (the latter used already twice, but inadvertently and therefore as an incorrect subsequent spelling, by FANG & ZHAO, 1992: 86), rather than coining long unpalatable nomina?

It is certainly praiseworthy for an author to have cared for a new nomen to be derived from an identified etymology (but then this should be done correctly: see DU BOIS, 2006c, 2007c), but this is much less important than the nomen being grammatically correct regarding its number (singular or plural according to the rank, see DU BOIS, 2009a) and being short, euphonious in all languages and “*easily memorable*”.

Scientific nomina are not an aim in themselves, but *tools* that are used in various contexts. Once coined, a new nomen will appear not only in taxonomic and phylogenetic publications, but also in all the scientific and non-scientific literature, in titles, official documents and lists, etc., published and distributed over the whole planet, that will deal with the organisms it designates. As such, it is much more important that nomina be short, simple and euphonious in all languages of the world than “full of meaning” and “strictly formed” from an etymological point of view. Because of the *rule of priority* and of the *nomenclatural founder effect* on which the nomenclatural rules are based (DU BOIS, 2005d), a nomen, once created, cannot be changed by subsequent authors and can be so only by a special intervention of the ICZN using its Plenary Powers, a very rare and heavy procedure. If it is the first one available for the taxon it designates, this nomen will have to be used by all authors who will deal with this taxon. When they are used in non-specialized literature, long and complex nomina are certainly not a good “publicity” for taxonomy, especially in our times when this scientific discipline is facing difficulties (WHEELER et al., 2004; PADIAL & DE LA RIVA, 2007). When coining new nomina, zootaxonomists should therefore care for those being short and simple.

This is particularly true for nomina designating “exceptional” or famous organisms, which will have to be mentioned hundreds of times in the non-specialized literature, on the web and in various other medias. This also applies to generic nomina that are at their creation, or are likely to become later, the basis for familial nomina. These considerations were clearly not taken into account by some authors who created long nomina for such recent discoveries.

The trend to coin long and unpalatable nomina is particularly obvious in the class AMPHIBIA, being even stronger for fossil taxa. Do we really need in zoological nomenclature specific nomina like *thoracotuberculatus* (8 syllables, 19 letters) or *acanthidiocephalum* (8 syllables, 18 letters), generic nomina like *Amphignathodontoides* (8 syllables, 20 letters) or *Saevesoederberghia* (9 syllables, 18 letters), familial nomina like PSEUDOPHELETHONTIDAE (10 syllables, 22 letters) or CALYPTOCEPHALIIDAE (9 syllables, 20 letters) or higher taxa nomina like HYDATINOSALAMANDROIDEI (11 syllables, 22 letters) or PALAEOBATRACHOMORPHA (9 syllables, 20 letters)? Taxonomists should also certainly avoid coining particularly highly repetitive nomina like *Ogalalabatrachus* (7 syllables, 16 letters). Although such nomina are indeed a very small minority among the many available nomina of AMPHIBIA, they tend to become more and more common, at least in some taxonomic groups. This can be exemplified by the generic nomina listed by FROST et al. (2006: 175, 213-214) in the families BUFOIDAE and SALAMANDRIDAE as recognized by them. The 50 nomina listed in their BUFOIDAE have from 4 (*Bufo*) to 16 letters (*Dendrophryniscus* and *Melanophryniscus*), with a mean of 11.3 and a median of 11.5. The 18 generic nomina listed in their SALAMANDRIDAE have from 6 (*Cynops*) to 15 letters (*Lycotalsalamandra*), with a mean of 10.7 and a median of 11.0, but if the 20 nomina of fossil genera of this family (ESTES, 1981; VINCEIT, 2008) are added, the maximum among the 38 nomina raises to 18 letters (*Cryptobranchichinus* and *Palaeosalamandrina*) and the mean to 11.6, the median remaining 11.0. The difference in the median number of letters between these two families is not significant (Mann-Whitney *U* test, $U = 928$, $P = 0.852$). In both families, a clear trend for an increase in the length of nomina over time since 1758 can be observed (fig. 1).

In contrast, the 37 nomina of RANIDAE listed by FROST et al. (2006: 248) only have from 3 (*Ama*) to 13 letters (*Pseudomalopsis*), with a mean of 8.5 and a median of 8.0. The difference between the BUFOIDAE and RANIDAE is highly significant (Mann-Whitney *U* test, $U = 705$, $P < 0.001$), and that between the SALAMANDRIDAE and the RANIDAE as well (Mann-Whitney *U* test, $U = 258.5$, $P < 0.001$). No clear trend for the increase in the length of nomina over time can be observed in the RANIDAE (fig. 1). This important difference is not due to chance. It is clearly related to the fact that rather numerous generic nomina of RANIDAE were coined rather recently, in particular in a paper by DUBOIS (1992), with the clear intention to make them short and simple – a point that has escaped the attention of most authors who have commented this work (e.g., INGAR, 1996). In contrast, the recent creation of many generic nomina of SALAMANDRIDAE and especially of BUFOIDAE, by several authors, was clearly made without any concern for this problem.

In our opinion, for the sake of communication with the whole community of zoologists and non-zoologists, this increase in the length of generic nomina in many families should not be encouraged, and future nomina to be coined should be short and simple. This is the case of the new nomina proposed below. As a rule of thumb, we would suggest that specific, generic and higher nomina should include a maximum of 8-12 letters (preferably less) arranged in

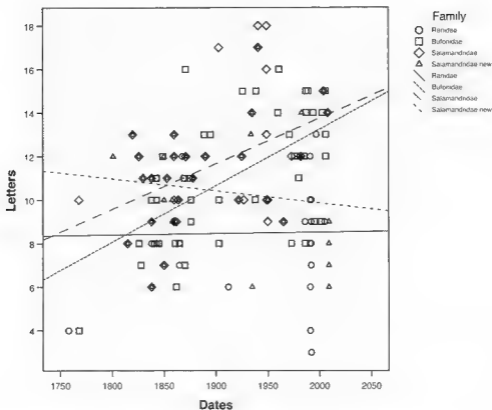


Fig 1 Numbers of letters in the genus-series nomina of three amphibian families (*BUFONIDAE*, *RANIDAE*, *SALAMANDRIDAE*) as recognized in FROST et al. (2006), with addition of the fossils in the *SALAMANDRIDAE* (see text), as well as in the ergotaxonomy of the family *SALAMANDRIDAE* adopted at the end of the present work ("Salamandridae new"). Each genus is plotted according to its number of letters and publication date, and regression lines over time of the number of letters are shown for the four groups of data.

4-5 syllables as defined above (preferably less), the latter being mostly composed of one or two consonant(s) and one vowel, as this is more likely to be euphonic in all or most languages. This should probably not become a "rule" of the *Code*, but it would be a useful addition to its "recommendations". This rule of thumb can be used as a guideline by all taxonomists working nowadays.

How can nomina be shorter and simpler, without completely losing their etymology and "meaning"? There are several ways to do so, four of which at least can be highlighted

(1) The use of more than two roots for a nomen should be avoided, as this always results in long nomina (*Allomevotriton*, *Brachytarsophrys*, *Pseudhymenochmus*)

(2) For coining nomina based on two or more different roots, nothing in the *Code* requires to combine the *complete* roots. Such nomina can validly be created by combining

parts only of the roots, as exemplified by many generic nomina of AMPHIBIA (e.g., *Afrana*, *Grohna*, *Kurixalus*, *Megophrys* or *Telmalsodes*), including several ones recently created in the URODELA (see e.g. PARRA-OLEA et al., 2004, McCranie et al., 2008). Generic nomina like *Lyciasalamandra*, *Nasikabatrachus* or *Paramesotriton* are unnecessary long. The virtually same nomina would aptly have been coined as "Lyciandra", "Nasikus" or "Paratriton" (none of which is preoccupied).

(3) Among several roots that carry the same message, preference should be given to the shortest and simplest one: e.g., in AMPHIBIA, "rana" instead of "batrachus" or "bufo" instead of "phrynus".

(4) An efficient way to reduce the length of nomina is to avoid adding long, useless endings to their basic root: thus, a specific nomen based on the name of a locality, region or country can well be coined by simply using the name of this place as it is, placed in apposition to the generic nomen, hence invariable. This avoids adding long endings in *-ensis*, *-ense*, *-cola*, *-icus*, *-ica*, *-icum*, *-ianus*, *-iana*, *-ianum*, etc. Additionally, this precludes potential grammatical mistakes of agreement in gender in case of transfer of the species to another genus. We think this should become a recommendation of the Code, and that its current Recommendation 11a, stating that "An unmodified vernacular word should not be used as a scientific name" should be suppressed. The recent decades have witnessed an unprecedented increase in the number of specific nomina ending in *-ensis*, especially in some countries, which provoke a real indigestion to people who are sensible to the aspect and length of nomina, and this should certainly change. We may be special, but we much prefer short specific nomina based on local geographical terms like *Aubria masako* (6 letters), *Colostethus roraima* (7 letters), *Phrynopis carpinis* (7 letters), *Rana diuata* (6 letters) or *Rana rara* (4 letters) to unpalatable ones like *Bolitoglossa guaramacalensis* (15 letters), *Crotaphatrema tchahambaboensis* (17 letters), *Megophrys wuliangshanensis* (16 letters), *Scutiger mokokchungensis* (15 letters), or *Hyalinobatrachium guararepanensis* (16 letters, not to mention the 17 letters of the generic nomen!).

A final recommendation that we would like to offer regarding the formation of new nomina concerns the grammatical gender of nomina of new subgenera. All the history of taxonomy since 1758 has shown a general trend in the progressive upgrading of ranks of taxa: what was a species in LINNAEUS (1758) has now often become a genus or a family, what was a family in LATREILLE (1825) has often become an order or a class, etc. This trend has accompanied the drastic increase in the number of named species and in our knowledge concerning the organisms. This upgrade in ranks poses no theoretical problems for taxonomy, as ranks do not carry any biological, evolutionary or other information and are purely arbitrary, just expressing the hierarchical structure of taxonomy and sister taxa relationships (DUBOIS, 2007a, 2008a). However, one of the results of this trend is that, regularly, subgenera or species-groups are elevated to the rank of genera. A particularity of zoological nomenclature is that specific epithets must agree in grammatical gender with their generic substantives. When a species is transferred from a genus to another whose nomen has a different grammatical gender, the ending of the specific nomen, if it is an adjective or a participle, must often be modified, and some zoologists have difficulties doing this, so that mistakes are regularly published in this respect. One possible way to avoid such errors is to care for new subgeneric nomina having the same grammatical gender as that of the nomen of the genus. We cared for

this below, but of course, when a subgeneric nomen is not a newly coined one but is transferred from another taxa or "resurrected", nothing can be done in this respect as this nomen cannot be modified

NUCLEOSPECIES DESIGNATIONS FOR GENERA

Nucleospecies ("type species") designations for genera are crucial acts in zoological nomenclature. Because the nomenclatural system of the *Code* is based on ostension using onomatophores and not on intensional definitions of taxa (see DUBOIS, 2005b, 2007a, 2008d), a genus nomen applies to any genus-series taxon including its nucleospecies, whatever diagnosis or definition of the taxon designated by this nomen had been given originally. Before working on the generic taxonomy of any zoological group, the first thing to do is therefore to identify the nucleospecies of all nominal genera referred to this group. We did this for the family *SALAMANDRIDAE* and we then realized that, just like for the family *RAVIDAE* a few decades ago (DUBOIS, 1981), among various nomenclatural errors repeated uncritically in the literature, a number of nominal genera still had no nucleospecies, and could therefore not be properly allocated to taxa. We therefore designate nucleospecies for all of them below.

The rules of the *Code* regarding nucleospecies designations require to follow a strict "order of precedence" among several possibilities (Art. 68). (1) original designation, (2) original monophory, (3) absolute tautonymy; (4) Linnaean tautonymy, (5) subsequent designation, (6) subsequent monophory. As defined by the *Code*, the situation (2) of original monophory should be strictly understood as meaning "including a single valid species", irrespective of the fact that this species may or not include several subspecies or synonyms (see below under *Neuregus*). These six possibilities are the only ones recognized by the *Code* for nucleospecies designation. This excludes for example designation "by implication" (see below under *Titinus*). The existence of an order of precedence among these possibilities means e.g. that if (1) applies, then (5) cannot apply, etc. The cases (3) and (4) are rare and apply only to old generic nomina published by Linnaeus or just subsequent workers. In the family *SALAMANDRIDAE*, only the cases (1), (2) and (5) are encountered. Attention has to be given to the fact that the choice of a nominal species for subsequent designation is limited to the "originally included species" of the nominal genus. As defined by the *Code* (Art. 67), these nominal species are either "those included in the newly established nominal genus or subgenus" (Art. 67 2 1) or, if no nominal species was originally included in it (which is acceptable until the end of 1930, Art. 13 3), "the nominal species that were first subsequently and expressly included in it" (Art. 67 2 2). This means that if a nominal genus was created without included species, any species can be subsequently included into it, even if described and named after this nominal genus. This precision is given here because we use this possibility below. Another important precision is that the "originally included species" cover all the nominal species listed by the original author as belonging in the genus, not only those considered valid by this author, i.e., also including the synonyms.

According to the *Code*, whenever several nomina are linked by a *relation of nonymy* (i.e., involving an archaonym and one or several neonyms subsequently proposed for it), all these nomina have by definition the same nucleospecies, whether this species was first designated as

nucleospecies for the archaenonym or for any of its neonyms (Art. 67.8). This rule also has consequences in the generic nomenclature of the *SALAMANDRIDAE*.

Finally, it must be stressed that, by definition, a neonym can have only one archaenonym. It is impossible under the *Code* to consider that a nomen has been proposed as a neonym for two or more distinct nomina (except in the improbable case where they would already all be linked by a relation of neonymy), as this would result in the same nomen having several distinct onomatophores and appearing in several distinct synonymies! A given nomen must be ascribed to a single synonymy, because, if it was indeed the synonym of several distinct nomina, this would mean that the latter also are synonyms³. Therefore, whenever a new nomen is published with a statement that it is meant at "replacing" two or more older nomina, this must be understood nomenclaturally as a double operation: (1) a subjective synonymisation of these two or more older nomina, (2) the creation of a new nomen for a new taxon and the inclusion of the two or more older synonyms in its synonymy. In the case of a new generic nomen thus proposed, its nucleospecies has to be established on the basis of the nominal species included in the new genus hence created.

THE NOMENCLATURAL STATUS OF WEBSITES DEALING WITH AMPHIBIA

Several websites are now available online dealing with the *AMPHIBIA*, including three very famous and useful ones. *Amphibian Species of the World (ASW)* below [http://research.amnh.org/herpetology/amphibia/], *AmphibiaWeb (AW)* [http://amphibiaweb.org/] and the *Global Amphibian Assessment (GAA)* [http://www.globalamphibians.org/]. Many batrachologists, zoologists and laymen use these three sites to find information about amphibians, and a tendency has developed in the recent years to quote these sites in scientific papers and to include their addresses in reference lists. This is problematic because websites, being labile in their content, cannot constitute permanent scientific bibliographic references (DUBOIS, 2003b). The same website can be consulted at different dates, and, except for a few persons who "followed" daily the site or stored its data in a way or another, there exists no possibility today to know what was the content of this site at the given date, even if this date is provided with the reference (which is not always the case). Thus for example, in the book of HERTHINS et al. (2003), two of the sites mentioned above are cited in reference lists of some contributions, as having been consulted at the following dates: *ASW* on 12 April 2002 (p. 94), 19 April 2002 (p. 130), 8 May 2002 (p. 117), 15 June 2002 (p. 88) and 19 November 2002 (p. 444), and *AW* on 12 April 2002 (p. 94), 8 May 2002 (p. 383) and 19 November 2002 (p. 443). It is impossible today for most "normal" users to have access to the original documents referred to by these "references". The latter may be useful to find a website providing some information, but this information changes with time, so they are useless as "references": to "publications" in fact, they simply amount to mentioning a "personal communication", a letter or a manuscript by a colleague, and as such they should not appear in bibliographical reference lists (DUBOIS, 2003b, 2004a).

³ There exists a rare exception to this situation: a species-series (nomen given to a specimen) that later is shown to be an interspecific hybrid must be referred to the synonymy of both its parent species. Two specific nomina in this case in the *Salamandridae*: *Triturus delislei* Drenth 1867 and *Triturus eximius* Peracca 1886. Both were created for specimens that were hybrids between *Triturus cristatus* Laurenti 1768, and *Triturus marmoratus* Lützelk. 1800, so these two nomina should stand in both their synonymies, but with a clear indication that they apply to interspecific hybrids, e.g. using the sign ×.

Although these sites always appear on top in any "Google search" and although many people think that they are more or less "official" and have the strong status of basic, unavoidable references, they are not. The *GAA* site is the only one to be in some way "official", as it presents the categories of threats of amphibian taxa as recognized by an international organization, the International Union for the Conservation of Nature (IUCN). The other two sites are only private sites, documented and maintained by private teams of people or even by a single individual. They are certainly very interesting and helpful to everybody, but the information they contain should never be taken for granted and uncritically accepted as valid or authoritative. This is clearly shown by the fact that all three websites present different, sometimes incompatible information, regarding the accepted phylogeny and taxonomy, the valid nomina of the taxa, the distribution of the species, etc.

This can be illustrated easily. In early November 2008, one of us (AD) just clicked on the name of the first country in the lists of countries of these three sites, which happens to be Afghanistan. The three sites provided different lists of amphibian taxa occurring in this country, with different nomina and distributions: 6 species in *GAA* (*Batrachuperus mustersi*, *Bufo stomaticus*, *Euphlyctis cyanophlyctis*, *Hoplobatrachus tigerinus*, *Paa sternosignata*, *Rana ridibunda*), 9 species in *AW* (*Bufo latastii*, *Bufo oblongus*, *Bufo pseudoraddei*, *Bufo stomaticus*, *Bufo variabilis*, *Euphlyctis cyanophlyctis*, *Paa sternosignata*, *Paradactylodon mustersi*, *Rana ridibunda*) and 11 species in *ASW* ("*Bufo*" *ohvaceus*, "*Bufo*" *stomaticus*, *Chrysopaa sternosignata*, *Euphlyctis cyanophlyctis*, *Hoplobatrachus tigerinus*, *Paradactylodon mustersi*, *Pelophylax ridibundus*, *Pseudepidalea oblonga*, *Pseudepidalea penzowii*, *Pseudepidalea pseudoraddei*, *Pseudepidalea turanensis*). The only nomen which appears identical in the three lists is *Euphlyctis cyanophlyctis*. The differences result either from simple nomenclatural disagreement, or from real taxonomic divergences, or from use of different distributional data on the species (in particular incorporating unpublished data, especially in *GAA*). Any user of these websites should therefore make his/her opinion about the information they provide, which often requires the recourse to external references. The contents of these sites should therefore never be considered as a "norm" that should necessarily be followed (e.g., regarding the valid nomina of taxa)⁴.

As concerns zoological nomenclature, these websites (as well as other similar ones) pose a particular problem: the new nomenclatural acts that they inevitably contain are not nomenclaturally available and should not be quoted in paper publications. As defined by the *Code* (Art. 8), to qualify as a "published work", a publication "must have been produced in an edition containing simultaneously obtainable copies by a method that assures numerous identical and durable copies" (Art. 8.1.3), and, if "produced after 1999 by a method other than printing on paper", it "must contain a statement that copies (in which it is published) have been deposited in at least 5 major publicly accessible libraries which are identified by name in the work itself" (Art. 8.6). These conditions exclude all works that are "published" only online, without a printed version.

Nomenclatural acts are of various kinds, e.g. *correction* of an incorrect original or subsequent spelling; *new combination* or more generally *new synonymy*; *change of ending*

4 Ironically, after these sites had been written, the third of the three websites mentioned above (*GAA*) closed (apparently 11 December 2008) and its content was transferred to another website (<http://www.tcreditt.org/amphibians>). We did not check whether the transfer was complete or not, and whether it implied content modifications or not, but this points to the relevance of our analysis above pointing to the "lability" of websites and their inappropriateness as permanent bibliographic references.

following a change of generic allocation for a species-series nomen or of rank for a family-series nomen, *designation* of a lectophoront (lectotype) for a species or of a nucleospecies for a genus; etc. Strictly speaking, most of these actions (e.g., the creation of a new combination) do not have “nomenclatural authors” but only *first-users* (Du Bois, 2000). Nevertheless, many checklists, catalogues and revisions provide the first-users of all onymorphs in their synonymies or *logonymies* (Du Bois, 2000), their authors should then refrain from crediting the new onymorphs to these websites, because they are nomenclaturally unavailable there, i.e., “non-existent” in zoological nomenclature. Any author who mentions an onymorph as having appeared in one of these sites becomes in fact, in strict nomenclatural terms, its first-user.

As tackled above, in our present discussion regarding salamandrid nomenclature, we are particularly concerned by the problem of nucleospecies designations for all nominal taxa that have not yet received such a designation. In this respect, the website *ASW* is particularly unreliable. The first version of this work, published as a book (Frost, 1985), contained a very high rate of errors and omissions (from 0.8 to 90.9% according to the kind of information, with a mean of 33.3% over 18 items) that required the publication of a long list of corrections (Du Bois, 1987b-c). Most of these corrections have been incorporated in the website, but many other “new” mistakes, especially errors in the synonymies, have been added, so that this website cannot be used blindly as a solid nomenclatural reference for amphibians.

Generic synonymies in *ASW* present information on past nucleospecies designations, but also sometimes unpublished data. Such new designations, or original “identifications”, of nucleospecies that appear in this site are nomenclaturally unavailable and should not be cited in serious taxonomic works. In other cases, *ASW* acknowledges the fact that no nucleospecies designation already exists for some generic nomina, and includes these nomina in several synonymies (those of the genera containing the originally included species of the nominal genus), which is highly confusing and nomenclaturally impossible, as shown above. The only proper allocation of a generic nomen that still does not have a nucleospecies is as an “incertae sedis” at the level of the higher taxon (tribe, subfamily, family, etc.) that is considered to include all its possible nucleospecies (e.g., all its originally included species).

Another related mistake consists in considering that a given generic nomen can be a neonym for several distinct older genera altogether, which is impossible for reasons explained above. Such nomina are in fact brand new nomina, and, if no subsequent nucleospecies designation has taken place, they must also be considered “incertae sedis”.

Finally, attention should be called to the fact that, besides these erroneous statements, some of the basic information given in *ASW* concerning some nucleospecies designations is incorrect, as exemplified below in several cases in the salamandrids.

For the time being, Art. 5 of the *Code* clearly states that a new nomen or nomenclatural act only published online has no nomenclatural availability, which is quite clear. Plans exist however to render available some nomina and acts published online *under particular conditions* (ANONYMOUS, 2008). Understanding these conditions may be easy for members of the ICZN or “professional taxonomists”, but not so for all laymen and unspecialized users of the web, who will be tempted to consider as “nomenclaturally available” any nomen or nomenclatural act gathered on the web. It is therefore easy to predict that, if these projects were indeed implemented, a period of nomenclatural confusion (if not chaos) will open, regarding which nomina, lectophoront or nucleospecies designations, are available and valid.

THE NOMINA CREATED BY DE LA CEPÈDE (1788a-b)

One of the major functions of the *Code*, as stated in its *Preamble*, is to “promote stability and universality in the scientific names of animals”. The ICZN, which is in charge of updating the *Code* and of dealing with problematic cases, often claims to care for “nomenclatural stability” and for this reason, in the recent years, has given more weight than in the past to “usage” against the Principle of Priority, which poses various problems that need not be discussed here (see DUBOIS, 2005a, 2008c). However, in some recent cases, this Commission has indeed taken decisions that go in the exactly reverse direction, for reasons that are difficult to understand, but which may have more to do with the egos of some persons than with a concern for “nomenclatural stability”. Thus, in the same period when this Commission “suppressed” a family-series nomen to “protect” a completely obscure tribe nomen that had been used *only 16 times* in zoological nomenclature since 1758 before the application for its conservation (DUBOIS, 1994, ANONYMOUS, 1997), the ICZN suddenly decided (ANONYMOUS, 2005) to deny nomenclatural availability to all the amphibian and reptilian nomina created in the very famous books by DE LA CEPÈDE (1788a-b), quoted thousands of times since their publication, despite clear warnings against “a rigid application of the Rules to old, well-known zoological works” (BOUR & DU BOIS, 1984) and despite “strong objection to the structure and content of the application” by one Commissioner.⁵ There is no doubt that, if all nomina in these two books had to be suppressed because of a few questionable species nomina not written under binominal form, although clearly included in genera, then many other nomina that have been in universal use for more than two centuries should also be “suppressed”. BOUR & DU BOIS (1984) gave the examples of the works of SCHLOSSER (1768) and BODDAERT (1770a-b, 1772a b), and an even more caricatural one can be mentioned (DU BOIS, 2005b: 426), the book of LAURENTI (1768), universally used as the starting point for the nomenclature of AMPHIBIA and REPTILIA, contains specific nomina that are fully unacceptable under the rules of the *Code*, such as “*Chamaeleo bonae spei*”, “*Coluber vipera anglorum*”, “*Vipera Francisci Radii*”, “*Vipera Moses Chatai*” or “*Constrictor rex serpentum*”. Certainly “suppressing” this book would in no way “promote stability in the scientific names of animals”, but the same was entirely true for DE LA CEPÈDE’s (1788a-b) books.

Be it as it may, we think that, to avoid the progressive implementation of a “nomenclatural chaos” which would no doubt result from all authors following “their own rules” (see examples in DU BOIS, 2006: 2007c, 2008a), zootaxonomists should care to follow strictly the *Code* and the decisions of the ICZN even when they were not in favour of the latter. Even if an overwhelming majority of them, if they had been consulted, would certainly not have agreed with the “suppression” of these books by a small team of “nomenclature specialists”, European herpetologists will now have to change their habits and stop using de la Cèpede’s nomina. In many cases, these nomina can be replaced by identical nomina used in BONNATERRE (1789), in a book that was largely derived from DE LA CEPÈDE’s (1788a-b) books, but in a few other cases this is not possible, when Bonnaterre had changed de la Cèpede’s nomina, which clearly results in nomenclatural instability.

⁵ As usual in the recent years (but not in the past: see DU BOIS, 2005f: 367-369), the deliberations of the ICZN being “secret”, the international community of zoologists was not informed of the nature of these “strong objections”, nor of the replies which could not be given to them in order to convince the Commissioners not to share them.

This is not the case, fortunately, in the *SALAMANDRIDAE*. Two species-series nomina coined by DE LA CÉPÈDE (1788*b*), that have been used in all checklists of species of this family and in all faunae of Europe or European countries for more than two centuries (e.g., MERTENS & WERMUTH, 1960*b*; THORN, 1969; THORN & RAFFAËLLI, 2001; RAFFAËLLI, 2007), must now be credited to BONNATERRE (1789) *Salamandra terrestris* and *Salamandra terdigitata*. In the latter case, the change is only one of authorship: the onomatophore (a single specimen kept in the Paris Museum under number MNHN 4658, THIREAC, 1986: 76) and the onymotope (Vesuvius, Italy) are not modified, as BONNATERRE (1789: 62) clearly stated that he had borrowed his description from DE LA CÉPÈDE (1788*b*). But the same does not apply to the nominal species *Salamandra terrestris*. For this species, DE LA CÉPÈDE (1788*b*: 194) considered a very wide distribution, including most of Europe (“*tant de pays de l’ancien monde, et même à de très-hautes latitudes*”), and did not state the origin of the specimens observed by him in the “*Cabinet du Roi*” (now the Paris Museum), so no precise onymotope was originally identified. EISLIT (1958: 136) designated Normandy (France) as “*terra typica restricta*”, but this onymotope restriction, followed by all authors until now, not being associated with a lectophoront or neophoront designation, is nomenclaturally void (DUBOIS & ÖHLER, 1995: 146, 1997: 312). BONNATERRE (1789: 62), when he redescribed the species under the nomen given to it by DE LA CÉPÈDE (1788*b*: 456), precised that he had written his description on the basis of two specimens he had observed on 11 October 1788 at Saint-Geniez en Rouergue (now Saint-Geniez-d’Olt, Aveyron, France, **valid onymotope**). Therefore, *Salamandra terrestris* Bonnaterre, 1789 has a precise onymotope, which is distinct from, and actually quite far from (about 600 km in straight line) that until now accepted for *Salamandra terrestris* de la Cépède, 1788. Very fortunately, both localities are included in the distribution currently accepted for the subspecies *Salamandra salamandra terrestris*, so this nomen remains the valid one for the same taxon.

THE NOMENCLATURE STATUS OF THE URODELAN GENERIC NOMINA CREATED BY RAFINESQUI (1815)

When it became consensual among batrachologists that the “*Triturus vulgaris* species group” should be recognized as a distinct genus, two different nomenclatural solutions to this problem were offered. MONTEBÀ & HERRERO (2004: 51) proposed to use the generic nomen *Lissotriton* Bell, 1839, whereas LIIVINCULK et al. (2005: 317) proposed to use the nomen “*Lophium* Rafinesque, 1815”. However, as noted by SCHMIDTTER (2004: 25), the latter nomen is a synonym, unavailable in zoological nomenclature. This is also true for RAFINESQUI’S (1815) nomina “*Aemus*” and “*Paludius*”, but not for his nomen *Triturus*, contrary to the statement by SCHMIDTTER (2004: 23), followed by SPILBRÖCK & CROCHÉ (2007). This deserves a few explanations.

In all his publications, and particularly in his 1815 work, RAFINESQUI rigorously used a very precise way of proposing his new generic nomina, with two distinct situations that have different nomenclatural consequences nowadays (DUBOIS, in preparation). All his new nomina were followed by the letter “R”, which means that he claimed authorship for them. But then some only were immediately followed by another generic nomen. This mode of notation, very common in taxonomic works at the beginning of the 19th century,

(see e.g. DUBOIS, 1987*d*), means that the new nomen was proposed as a neonym for the following one. However, some other new nomina in RAFINESQUE (1815) were neither followed by another generic nomen, nor by the nomina of included species, nor by a diagnosis or description of the genus: such nomina are indeed gymnomyms, unavailable in zoological nomenclature.

RAFINESQUE (1815: 78) listed five genera in his family TRITONIA, as follows "G. 1. *Triturus* R. *Triton* Dum. 3 [for 2] *Salamandra* Lac. 3 *Palmitus* R. 4. *Lophinus* R. 5. *Meinus* R. [sic]". There is a single, straightforward, interpretation of this presentation: (1) he recognized the genus *Salamandra* as used by DE LA CLIPÈDE (1788*b*: 456), which is in fact a subsequent usage of the generic nomen *Salamandra* Laurenti, 1768; (2) he proposed the neonym *Triturus* for the generic nomen *Triton* as used by DUMÉRIL (1806), which is in fact a subsequent usage of the generic nomen *Triton* Laurenti, 1768, this neonym is fully available in zoological nomenclature; (3) he proposed three gymnomyms, "*Lophinus*", "*Meinus*" and "*Palmitus*": being devoid of any description, indication or mention of nominal species included in the taxon, these three nomina are unavailable in zoological nomenclature.

FITZINGER (1843: 34) designated *Triton cristatus* Laurenti, 1768 as nucleospecies of *Triton* Laurenti, 1768. Thus doing, he also designated the nucleospecies of all the neonyms proposed by subsequent authors for the latter nomen for its being preoccupied by *Triton* Linnaeus, 1758 (Mollusca), which are four in number, *Triturus* Rafinesque, 1815; *Molge* Merrem, 1820; *Oracurus* Leuckart, 1821; and *Tritonella* Swainson, 1839 (a nomen ignored by most authors until now e.g., GARCÍA-PARÍS et al., 2004). All these nomina are objective synonyms and the valid nomen of the genus including *Triton cristatus* Laurenti, 1768 is *Triturus* Rafinesque, 1815.

Despite their being nomenclaturally unavailable, the three other nomina created by RAFINESQUE (1815) need nucleospecies, in order to be allocated to the synonymy of a single valid nomen (see below). Fortunately, despite the absence of diagnoses and included species, clues exist for the designation of these nucleospecies.

First of all, we are guided by the fact that one of these three nomina was "validated" later on, by GRAY (1850: 27), who recognized a genus *Lophinus* and provided a diagnosis for it, thus making it nomenclaturally available. Although GRAY (1850: 27) expressly credited this nomen to "Rafinesque", the latter is not the nomenclatural author of the nomen. The *Code* expressly states that the author of a nomen is not the person who coined it but "the person who first publishes it () in a way that satisfies the criteria of availability" (Art. 50.1). GRAY (1850: 26-28) referred two nominal species to his new genus *Lophinus*: *Salamandra punctata* Latreille, 1800 and *Salamandra palmata* Schneider, 1799. None has been subsequently designated as nucleospecies, so that proper taxonomic allocation of this nomen has remained impossible until now. We hereby designate the nominal species *Salamandra punctata* Latreille, 1800: 31 as the nucleospecies of both "*Lophinus*" Rafinesque, 1815 and *Lophinus* Gray, 1850 (**new nucleospecies designations**). These two nomina are therefore now linked by an objective synonymy, and they are both invalid objective **new synonyms** of *Lissotriton* Bell, 1839 (nucleospecies, *Salamandra punctata* Latreille, 1800, by subsequent designation of FITZINGER, 1843: 34).

As for the other two gymnomyms created by RAFINESQUE (1815), they were not "validated" by subsequent authors, but they may be so or might be so in the future. This may be

useful in case of need to recognize additional genus-series taxa within the group of European newts, e.g. for taxa at rank subgenus or even at lower ranks such as infragenus, should the *Code* later allow the use of such ranks. In such cases it will be useful to know the nucleospecies of RAFINESQUE'S (1815) nominal taxa, in order to use the same nucleospecies for the same nomen once validated by publication of a diagnosis, definition or description. For this reason we here designate nucleospecies for these two gymnonyms.

By itself, the nomen "*Palmatus*" Rafinesque, 1815 (not mentioned in *ASW*) suggests that it was intended for the palmate newt. We hereby designate the nominal species *Lacerta helvetica* Razoumowsky, 1789, 111, its now valid nomen, as nucleospecies of this gymnonym (**new nucleospecies designation**). The latter is not "revalidated" here, but could be useful for "revalidation" if this species had to be taxonomically separated, as some level of the genus-series, from the other species of *Lissotriton*. For the time being, this gymnonym has to stand in the synonymies of the latter nomen (**new synonym**), both as genus and subgenus.

As for the nomen "*Meinus*" Rafinesque, 1815 (listed in *ASW* as a synonym of both *Lissotriton* and *Triturus*), we indeed "revalidate" it below, for a subgenus of *Lissotriton*.

PROPOSED TAXONOMIC CHANGES IN THE FAMILY SALAMANDRIDAE

We identified taxonomic problems at different levels in the family SALAMANDRIDAE. After a brief presentation of these problems, we offer new taxonomic and nomenclatural proposals for this family. With the data currently available, all the taxa we recognize appear to correspond to robust holophyletic groups.

SUBFAMILIES

Several authors in the past have recognized two major groups in the SALAMANDRIDAE: the "true salamanders" (SALAMANDRINAE) and the "newts" (PLEURODELIINAE). However, recent works, based on both molecular (LARSON, 1991; TITUS & LARSON, 1995; LARSON et al., 2003; MONTORI & HERRERO, 2004; WISROCK et al., 2005, 2006; STIENJARTZ et al., 2007; ZHANG et al., 2008) and skeletal (VENCZIL, 2008) data, suggest that the genus *Salamandrina*, and possibly the poorly known fossil genus *Archaeotriton*, should be recognized as a third distinct lineage (RAFFAELLI, 2007: 150, 343), the "spectacled salamanders". This is acknowledged below by the erection of a third subfamily (for which the nomen SALAMANDRINAE is already available) for these two genera.

TRIBES, SUBTRIBES AND INFRATRIBES

Within subfamilies, the situation is rather simple concerning the relationships within the "true salamanders" (SALAMANDRINAE). All recent molecular studies (TITUS & LARSON, 1995; VITTI et al., 1998; WISROCK et al., 2001, 2006; STIENJARTZ et al., 2007; ZHANG et al., 2008) confirm the existence of two main holophyletic groups within this subfamily: *Salamandra* and

Lyctasalamandra (that may be called “stout salamanders”), and *Chioglossa* and *Mertenstella* (“slim salamanders”) These two groups are here taxonomically recognized as tribes.

The situation is more complex regarding the “newts” (*PLEURODELINI*). They have often been considered to consist in two major groups. The first one, called “primitive newts” by ZHANG et al. (2008), includes the Palaearctic genera *Pleurodeles*, *Tylostotriton* and *Echnotriton* and related fossil genera, whereas the second one, unnamed by STEINFARTZ et al. (2007) and ZHANG et al. (2008) but that may be called “modern newts”, includes the other Palaearctic and the two Nearctic genera (ESTES, 1981; HAYASHI & MATSUI, 1989; TITUS & LARSON, 1995; LARSON et al., 2003; MONTORI & HERRERO, 2004; VEJTH et al., 2004; FROST et al., 2006; WISROCK et al., 2006; STEINFARTZ et al., 2007; ZHANG et al., 2008). These two groups can be taxonomically recognized as two tribes, whose valid nomina are *PLEURODELINI* and *MOLGINI* (DUBOIS, 1985).

Recent works (HAYASHI & MATSUI, 1989; WISROCK et al., 2001, 2005, 2006; MONTORI & HERRERO, 2004; STEINFARTZ et al., 2007; ZHANG et al., 2008) suggest the existence of several holophyletic subgroups within the latter tribe. We propose to recognize taxonomically these finer subdivisions as subtaxa within the *MOLGINI*.

The first dichotomy within the “modern newts” is between the two Nearctic genera *Notophthalmus* and *Taricha* and all the other genera. The North American group, the “New World newts” of STEINFARTZ et al. (2007) and ZHANG et al. (2008), already identified by HAYASHI & MATSUI (1989), is strongly supported in several recent analyses (WISROCK et al., 2005, 2006; FROST et al., 2006; STEINFARTZ et al., 2007; ZHANG et al., 2008), and is here recognized as a new subtribe. The second subtribe *MOLGINI*, the “modern Eurasian newts” of STEINFARTZ et al. (2007), is also well supported (FROST et al., 2006; WISROCK et al., 2006; STEINFARTZ et al., 2007; ZHANG et al., 2008). It contains several groups that appear holophyletic in all recent analyses, but their mutual relationships are not yet fully clarified, which does not allow to establish a taxonomic hierarchy between them (see above). Pending the resolution of these relationships, we only recognize some members of this polytomy as three taxa of the same family-series rank, as infratribes of the *MOLGINA*.

The first infratribe, the “Corso-Sardinian newts” of ZHANG et al. (2008), consists in a single genus, *Euproctus*, as redefined by CARRANZA & AMAT (2005). This distinctive holophyletic group, already recognized by CACCONI et al. (1994, 1997), was nested among the group including all other European genera in several recent works (MONTORI & HERRERO, 2004; CARRANZA & AMAT, 2005; STEINFARTZ et al., 2007), but appeared as the sister-group of all other European newts in the analyses of WISROCK et al. (2006) and ZHANG et al. (2008).

The second infratribe, the “modern Asian newts” of STEINFARTZ et al. (2007) and ZHANG et al. (2008), includes *Cynops* and all other East Asian genera of the subtribe *MOLGINI*. It has been well supported as a holophyletic group in several studies using different methods (HAYASHI & MATSUI, 1989; TITUS & LARSON, 1995; CHAN et al., 2001; FROST et al., 2006; WISROCK et al., 2006; STEINFARTZ et al., 2007; ZHANG et al., 2008), but its relationships with the other European genera is not consensual among them.

The third infratribe, the “modern European newts” of ZHANG et al. (2008), includes all the remaining European newt genera. Although it came out as a well supported holophyletic group in the analysis of ZHANG et al. (2008), this group appeared as paraphyletic in all other

recent analyses (CARRANZA & AMAT, 2005, WISROCK et al., 2006; STEINFARTZ et al., 2007) and may have to be dismantled when the cladistic relationships among its genera and with the East Asian ones, which are still controversial, are better understood. Given the uncertainties that remain regarding the cladistic relationships between its genera, we consider it premature to recognize formal taxonomic groupings above genus within this infratribe (see also below the problems posed by the data on hybridization).

GENERA AND SUBGENERA

Stout salamanders

This group contains a high number of species and is likely to be dismantled in the future. STEINFARTZ et al. (2000), ESCORIZA et al. (2006) and WISROCK et al. (2006) provided convincing molecular evidence for the existence of at least six holophyletic groups in this complex. We here treat them taxonomically as subgenera. Although this may appear premature to some, a major reason for our doing so is to avoid the repetition of the unfortunate creation of long unpalatable nomina like *Lyciasalamandra* for these taxa. We therefore propose below short, "compressed" nomina for the subgenera of *Salamandra*.

New World newts

The molecular data of WISROCK et al. (2006) provide strong support for the existence of two holophyletic groups in each of the two Nearctic genera *Nothophthalmus* and *Taricha*. We here recognize two subgenera in each of these genera.

Modern Eurasian newts

Within this group of the "true newts", several recent works based on molecular cladistic data have resulted in important taxonomic changes regarding the traditional European genera *Triturus* and *Euproctus*, with recognition of several distinct genera (MONTORI & HERRERO, 2004, GARCÍA-PARIS et al., 2004, CARRANZA & AMAT, 2005; LITVINCHUK et al., 2005). These taxonomic decisions are supported by the recent analysis of ZHANG et al. (2008). We follow them here although we have reservation about the rank genus given to several of the newly recognized taxa (see below). Anyway, if this genetic taxonomy is adopted, simple taxonomic consistency and homogeneity then requires also bringing changes to the taxonomy of the traditional East Asian genera *Cynops* and *Paramesotriton*.

Based on cranial characters, ZHAO & HU (1984, 1988) recognized three species-groups in the genus *Cynops*: a Japanese one, with the species *pyrrhogaster* and *ensicauda*, and two Chinese ones, with all other species. CHAN et al. (2001) suggested that this genus is paraphyletic, its Japanese species being more closely related to the genera *Paramesotriton* and *Pachytriton* than to its Chinese species, and that, if these results were confirmed, "an appropriate taxonomic resolution would be to recognize the genus *Hypselotriton* Wolterstorff, 1934 as a valid taxon containing at least *cyanurus* and *wolterstorffi*" (CHAN et al., 2001: 1005). WISROCK et al. (2006: 380) did not find support for the paraphyly of *Cynops*, but they wrote that "this grouping is not well supported by either Bayesian or parsimony analyses". Their

results are congruent with the holophyly of both the Japanese and Chinese groups of this genus, which was again confirmed by STEINFARTZ et al. (2007) and by ZHANG et al. (2008). Here, we restrict the genus *Cynops* to the Japanese species and we place all Chinese species in the genus *Hypselotriton*. This genus is here understood with a wider extension than in several recent Chinese publications (e.g., FEI et al. 1990, 2005, 2006; YE et al., 1993, FEI, 1999) where it accommodated only the species *wolterstorffi*, whereas all other species of this group were maintained in *Cynops*.

Following ZHAO & HU (1984, 1988), two well-identified groups at least can be recognized in this genus, the *wolterstorffi* group (with the species *chenggongensis*, *cyanurus* and *wolterstorffi*) and the *orientalis* group (with *orphicus* and *orientalis*). We recognize these two groups as subgenera of *Hypselotriton*. The nomen *Pungia* Chang, 1935 is available for the second subgenus. This nomen is based on the nucleospecies *Pachytriton granulatus* Chang, 1933. The holophoront of this species being lost, its identity has long been uncertain: some authors (e.g., THORN, 1969; THORN & RAFFAELLI, 2001) considered it as a synonym of *Cynops orientalis*, others (e.g., FEI et al., 2006, RAFFAELLI, 2007) as a synonym of *Pachytriton labiatus*, and others (e.g., YE et al., 1993; ZHAO & ADLER, 1993) simply ignored it. This species was recently rediscovered in the field by HOU et al. (2009), who provided a redescription, measurements and photographs. Based on these new data, we agree with CHANG (1936) in considering these specimens as belonging in a species close to, although distinct from, *Hypselotriton orientalis* (David, 1875), and not in the genus *Pachytriton*. As stated by the latter author, this is most likely also the species collected by Pope in 1921 in Anhwei and considered by SCHMIDT (1927: 555) as a "terrestrial stage" of *Triturus orientalis*. *Hypselotriton granulatus* (new combination) is distinguished from *Hypselotriton orientalis* by its being slightly larger (total length up to 96 mm versus 90 mm in *orientalis*), its very tuberculate dorsal skin (versus slightly granular in *orientalis*), with minute glands on the dorsum and the head, its orange red spots along each side (no spots or very few on the sides of *orientalis*) and its big orange-red blotches on the ventral surface (smaller red blotches in *orientalis*). Both species occur in Zhejiang.

The genus *Paramesotriton*, as traditionally understood, is also heterogeneous. The recently described species *laevis* shows strong both morphological and well-supported molecular divergence from all other species of the genus and also to the genus *Pachytriton*, appearing as the sister-group to the cluster of these two genera (WEISROCK et al., 2006, 378) or to the genus *Pachytriton* (ZIANG et al., 2008). This indeed suggests that it "should not be placed in the genus *Paramesotriton*" (WEISROCK et al., 2006, 380). We here refer this beautiful and distinctive species to its own genus, for which we provide a nomen. Within the remaining group, both morphological (CHAN et al., 2001) and molecular (WEISROCK et al., 2006) data suggest that the species *caudopunctatus* represents a distinct holophyletic group, sister to the cluster of the remaining species. We here place it in a distinct subgenus, for which a nomen is already available (RAFFAELLI, 2007: 128).

In the European genus *Triturus*, two "species-complexes", *cristatus* and *marmoratus*, have long been recognized, and they are supported by all recent analyses (MAC GREGOR et al., 1990; MIKULIČIĆ & PÍLÍK, 2003; MONTEI & HERRERO, 2004; CARRANZA & AMAL, 2005; WEISROCK et al., 2006; STEINFARTZ et al., 2007). We recognize them taxonomically below as two subgenera, for which nomina are already available. Similarly, we recognize as subgenera the two "clades" (northern and southern) within the genus *Neurergus*, separated since 11 Mya according to STEINFARTZ et al. (2002).

In the genus *Lissotriton*, WEISROCK et al. (2006) identified two distinct groups, one with *Lissotriton boscai* and one with all other species, which we here recognize as subgenera. PLICIO & RAFINSKI (1985) pointed to the absence of "whip and wave" during the male nuptial dance of *Lissotriton boscai*, whereas these behaviours are present in all other *Lissotriton* species, although very attenuated in *Lissotriton italicus*. The genus *Ichthyosaura* also lacks whip and wave, and this absence is clearly a plesiomorphic character.

A particular problem would be posed by the implementation of the mixogenus concept, as defined above, in the group of the modern European newts. For most of the 20th century, many authors realized artificial hybridization experiments between all the species that were then placed in a single genus *Triturus* (see subcomplete lists of references in MANCINO et al., 1978 and in MACGREGOR et al., 1990: 339-340). According to these works, adult hybrids were obtained between various species, not only of the same genus according to the current generic taxonomy of these newts, but also belonging to different genera *Ichthyosaura* and *Lissotriton* (SCHREITMÜLLER, 1910; WOLTERSTORFF, 1925: 280, 289; BATAILLON, 1927; BATAILLON & TCHOU SU, 1932; LANIZ, 1934; PARISER, 1935, 1936; MANCINO et al., 1976; MACGREGOR et al., 1990), *Ichthyosaura* and *Ommatotriton* (MACGREGOR et al., 1990), *Ichthyosaura* and *Triturus* (BATAILLON, 1927; BATAILLON & TCHOU SU, 1932; PARISER, 1935, 1936), *Lissotriton* and *Triturus* (POLL, 1909; WOLTERSTORFF, 1909a-b, 1910, 1911, 1925: 279; BATAILLON, 1927; BATAILLON & TCHOU SU, 1932; PARISER, 1932, 1935, 1936; HAMBURGER, 1935; MANCINO et al., 1976, 1977, 1978, 1979; MACGREGOR et al., 1990), and *Lissotriton* and *Ommatotriton* (WOLTERSTORFF, 1925: 279; MACGREGOR et al., 1990). For the oldest works, no data are available on the ploidy and characters of these specimens, that would allow to ascertain that they were indeed diploid adult hybrids, but such data exist in the recent works. Thus, MANCINO et al. (1977) reported in detail about diploid adult hybrids between *Lissotriton meridionalis* and *Triturus carnifex*. Certainly this question should be studied again, but, given the current disinterest of taxonomists for hybridization (DUBOIS, 1998a), we may have to wait for a while until fresh detailed data are available.

If all the "intergeneric" adult hybrids liable to be produced, at least in artificial conditions, between these groups, proved to be real diploid hybrids, adopting the mixogenus concept would require to downgrade all four genera *Ichthyosaura*, *Lissotriton*, *Ommatotriton* and *Triturus* to the rank of subgenera of a single genus *Triturus*. Furthermore, if the cladistic relationships within modern newts presented by WEISROCK et al. (2006) and ZHANG et al. (2008) were confirmed, the genera *Calotriton* and *Neurergus* should also be treated as subgenera of *Triturus*, for simple reasons of cladistic consistency (see DUBOIS, 2004b). The current subgenera recognized below in some of these genera should then be downgraded to the rank of supraspecies (or later of infragenera if this rank is subsequently authorized by the Code). This would contradict the recent trend which has led to the upgrading of the species groups of *Triturus* to separate genera. The taxonomist community is a very conservative one, and changes take time to be eventually accepted. It is unlikely that time is ripe for the salamander taxonomists of today to lump again what they have been splitting in the recent years. For this reason, and also because detailed information on the ploidy and chromosomal complement of most of these "intergeneric" hybrids is still wanting, we do not implement these consequences of the reported crosses in our taxonomy, but we wish to stress that this would not at all be shocking and unacceptable. It would not exactly amount to coming back to the generic taxonomy that has long prevailed for European newts, as it would require the

inclusion of a few additional groups in the genus *Triturus*. It would simply result in a change of rank for the taxon recognized by RAFFAELLI (2007) as the supergenus *Triturus* and below as the infratribe *MOLGITA*, but without modifying its content and taxonosis, nor those of its included taxa

Primitive newts

Within the genus *Tylotriton*, two well-supported holophyletic groups have been identified by WEISROCK et al. (2006). They correspond to the *asperimus* and *verrucosus* species groups as recognized by FEI (1999) and FEI et al. (2005, 2006), and they are supported by clear behavioural differences. They are recognized here as two subgenera

In this group also, a particular problem would be posed by the use of the mixogenus concept. FERRIER et al. (1971) reported having obtained hybrid specimens between females of *Pleurodeles waltl* and males of *Tylotriton verrucosus*. FERRIER & BEITSCHEN (1973) later reported that some of these hybrids of both sexes (numbers not given) reached the adult stage. In particular, the males had nuptial pads. However, they failed to obtain reproduction from these hybrids. Since that date however, no adult hybrid between these genera was reported, although these newts have been raised in captivity by several amphibian breeders.

On the basis of these successful crosses, DUBOIS (1982, 1987a) suggested that *Tylotriton* and *Echmotriton* should be considered subgenera of *Pleurodeles*. Whereas at the time of WOLTERSTORFF (1925) or LANTZ (1947) such a suggestion would probably have been followed, it is interesting to note that, since 1982, not one author seems to have adopted this taxonomic proposal, despite the comments of BUCCI-INNOCENTI et al. (1983) on the use of artificial hybridization results in taxonomy. For this reason, which in our opinion reflects rather the "conservatism" of the taxonomic community mentioned above, than a clear "genus concept" alternative to that of mixogenus, we here maintain these taxa at the rank of genera. However, we suggest that in the future the possibility to downgrade *Pleurodeles* and *Tylotriton* to the rank of subgenera of a single genus *Pleurodeles* should be seriously considered. Besides, as *Pleurodeles* seems to be the sister-taxon of the group *Echmotriton* + *Tylotriton* (WEISROCK et al., 2006; ZHANG et al., 2008), this would imply also considering *Echmotriton* as a third subgenus of *Pleurodeles* for mere reasons of cladistic consistency (see DUBOIS, 2004b), and the latter genus should perhaps include also some of the fossil genera currently recognized in the tribe *PLEURODELEINI* (see table 5). If *Tylotriton* was to be downgraded to the rank of a subgenus of *Pleurodeles*, the two subgenera here recognized in *Tylotriton* should be downgraded to the rank of supraspecies, respectively *verrucosus* for *Tylotriton* and *asperimus* for the new subgenus defined below. Hopefully also, in the future, the *Code* will allow for the use of a rank infragenus, which would allow to have a more expanded hierarchy of genus-series ranks below genus and might make it easier to abandon the "genera" *Tylotriton* and *Echmotriton*.

SUPRASPECIES, SPECIES, EXERGES AND SUBSPECIES

We presented above the criteria that we use to recognize taxa of rank species. In some situations, this leads us to elevate some former subspecies to the rank species, quite in the line of the suggestions of HIGHTON (2000)

In a few cases, we use additional ranks around the rank species to account for rather detailed relationships between species and subspecies inferred from recent data: in one case, we group closely related species in one subgenus as taxa of the rank supraspecies, as defined above (for “aggregate of species” in the *Code*), whereas in two other cases we recognize taxa of the rank *exerge* (for “aggregate of subspecies” in the *Code*).

These guidelines result in taxonomic changes at low levels in three groups, the stout salamanders and two genera of modern European newts, the Alpine newts and the smooth newts.

Stout salamanders

We here elevate some former subspecies of some subgenera of the genus *Salamandra* to species level, whereas in other cases the information currently available is too scanty to do it for the time being.

The North African subgenus contains at least four very different “groups of populations” (STEFANIARTZ et al., 2000; DONAIRI BARROSO & BOGAERTS, 2003; ESCORIZA et al., 2006): one in eastern Algeria (including the mount Edough near Bôna, onymotope of the current subspecies *S. a. algira*), one in western Algeria and eastern Morocco (including the Beni Snassen mountains, onymotope of the current subspecies *S. algira spelaea*, and one west Algerian population currently referred to *S. a. algira*), one in the central Rif mountains and the Middle Atlas in Morocco (currently referred to *S. a. algira*), and one in the Tingitania region in extreme northern Morocco (*S. algira tingitana*). According to STEFANIARTZ et al. (2000), the genetic difference between the onymotopic population of *algira*, and that of Chefchaouen in the Rif, is very high, suggesting probable specific differentiation. However, ESCORIZA & COMAS (2007) stated that the Beni Snassen population (*spelaea*) is more closely related to eastern Algerian populations than to the nearby population from the central Rif mountains. We therefore propose to recognize three distinct species, *Salamandra tingitana* (**new onymorph**) for the Tingitania populations, *Salamandra algira* with two subspecies (*algira* and *spelaea*), and a still unnamed species in the Rif and the Middle Atlas. The species *tingitana* is easily distinguished from the other two species by its very different morphology, its viviparous mode of reproduction and its different ethology, as shown by its special requirements in captivity.

The subgenus of the Near East is composed of at least four different “groups of populations” (STEFANIARTZ et al., 2000), but their current assignment to the subspecies already named is still impossible due to the lack of clear delimitation of the populations and of insufficient molecular work. Here we simply use the traditional subspecific taxonomy of three subspecies within a single species *inframaculata*, but this group requires revision.

In the Alpine subgenus, on the basis of the data of STEFANIARTZ et al. (2000), RIBIRON et al. (2004), BONATO & STEFANIARTZ (2005) and Veronique Heltzer (personal communication), we consider *Salamandra atra* and *Salamandra atrae* (**new onymorph**) as two distinct species, with three subspecies in the former species. In contrast with these authors, we recognize the subspecies *peninsularis* from Bosnia & Herzegovina, Serbia, Montenegro and Albania, because it is isolated from the other populations in the non-Dinaric Alps and shows morphological differences from them, being smaller and slightly different in coloration. Its vulnerability fully justifies its formal taxonomic recognition.

Specific and intraspecific differentiation is high within the hyponymous subgenus *Salamandra* as here defined. Recent analyses (STEINFARTZ et al., 2000, GARCÍA-PARÍS et al., 2003, ESCORIZA et al., 2006, WEISROCK et al., 2006) allowed to identify several holophyletic groups in this group, which are here taxonomically recognized at different levels. We recognize three species, three exerges (aggregates of subspecies) and twelve subspecies within this taxon. The various taxa within this complex can be arranged in three major groups.

The first group, from southern Spain, includes, in our view, a good species, *Salamandra* (*Salamandra*) *longirostris* (**new onymorph**), and two subspecies of the hyponymous species. The former is an ancient isolated population considered basal to other *Salamandra* and close to the African North African salamanders, from which it is only separated by the Gibraltar strait (GARCÍA-PARÍS et al., 2003). *Salamandra longirostris* (**new onymorph**) is a species of medium size, with many yellow spots. It is ovoviviparous but has a short aquatic larval period. It is striking in showing low adaptability in captivity (personal observations, JR). The two subspecies *respoi* and *morenica* still show intergradation with more northern subspecies of *Salamandra salamandra* (GARCÍA-PARÍS et al., 2003) and thus do not deserve to be recognized as species. We include them in an exerge (*respoi*) of the species *S. salamandra*.

The second group defined by STEINFARTZ et al. (2000) and supported by the data of HIGHTON (2000) and GARCÍA-PARÍS et al. (2003) contains two subgroups that are molecularly close to one another but more remote from the third subgroup with which they are in contact in some populations. These two subgroups are most likely remnants of an old lineage. They are very disjunctive geographically, one (*giglioti*) being found in southern Italy, and the other one (*alfredschmidti*, *bernardeti* and *fastuosa*) in northern Spain and southwestern France. Although morphologically distinct, these taxa do not seem to be reproductively isolated from the subspecies of *S. salamandra* with which they are in contact and thus do not deserve to be recognized as distinct species. We group these four subspecies in an exerge *fastuosa* of the species *S. salamandra*.

The third and last group defined by STEINFARTZ et al. (2000) contains the remaining six subspecies, as well as *Salamandra* (*Salamandra*) *almanzoris* (**new onymorph**) from central Spain, which we here elevate to species level (see also GARCÍA-PARÍS et al., 2003; MARTÍNEZ-SOLANO et al., 2005). It is also considered as a relict unit with a special evolutionary history ("ESU", see above), and is currently in competition with a more modern population (*bejarae*) coming from the North. *Salamandra almanzoris* (**new onymorph**) has a small size, with a rather slender habitus and very few yellow spots. It is ovoviviparous with a long aquatic larval period, and remains very aquatic in the adult stage (CAHILL, 1963). It shows low adaptability in captivity and is very different morphologically from the nearby populations of *bejarae*.

As a whole, *Salamandra* (*Salamandra*) *salamandra*, as here restricted, is a species from southern and central Europe, with a small to large size, and many yellow spots or yellow bands. It is ovoviviparous or viviparous. It shows high adaptability in captivity.

Alpine newts

The recent data of SOTIROPOULOS et al. (2007) suggest the existence of three well-supported different holophyletic groups in the species *Ichthyosana alpestris*, which in our opinion should be recognized taxonomically. These are a relict group (A) represented in

south-eastern Serbia, a western European group (B-C) and an eastern European group (D-E). Both these latter groups can further be divided into two groups each, respectively (B) and (C), and (D) and (E). The data of these authors do not suggest the recognition of several species, although we consider it very likely that some of the taxa discussed below will have to be raised to species level when more data are available. It is impossible at this stage to provide a complete infraspecific taxonomy of this species, because species-series nomina are lacking for some taxa that should be recognized as subspecies. SOTIROPOULOS et al. (2007, 2008) failed to describe and name the subspecies from south-eastern Serbia, from north-eastern Italy and from Greece uncovered by their analysis. We just provide here brief guidelines for the taxonomy of this group.

We think that this species should be divided in at least three exerges, possibly five. It will be possible to name the first exerge only when the populations of group (A) have been formally described and named as a new subspecies: its nomen will also provide the nomen for the exerge. For the time being, we suggest to recognize only two exerges for the other two groups, but a finer analysis may require further splitting.

The western European group (B-C), the *alpestris* exerge, includes at least five groups of populations that deserve in our opinion the status of subspecies. An Italian group (B) includes the subspecies *Ichthyosaura alpestris apuana* (**new combination**) and *Ichthyosaura alpestris inexpectata* (**new combination**). Contrary to SOTIROPOULOS et al. (2007), we maintain the latter as a valid taxon because of geographic discontinuity between this subspecies and *apuana*, of the morphological (DUBOIS & BRUIE, 1983) and genetical (BRUIE, 1983, 1986; ANDREONE, 1990) differences between them, and because its bearing a distinct Latin nomen provides support for the conservation of this very small and endangered isolate, known only from four populations (DUBOIS, 1998b). A northern Spanish group (C1) corresponds to the subspecies *Ichthyosaura alpestris cveri* (**new combination**). No nomen is clearly available for a subspecies that should be recognized for the populations of north-eastern Italy that came out as a well-supported group (C2) in the analysis of SOTIROPOULOS et al. (2007). The nomen *Triton alpestris lacustris* Seliškar & Pehani, 1935, and its synonym *Triton alpestris lacustris* Seliškar & Pehani, 1935, created for populations of Slovenia, might however possibly apply to this taxon. Finally, the nomen *Ichthyosaura alpestris alpestris* (**new combination**), which has several synonyms, applies to the subspecies (C3) that straddles northern and central Europe from France to northern Romania.

Because of the Rule of Priority applying to "aggregates of subspecies", the eastern European group (D-E) must bear the nomen of *reisei* exerge. It first includes a group (D), mostly from Greece, among which several subgroups (D1) to (D4) were clearly identified (SOTIROPOULOS et al., 2007, 2008), but for which a single nomen, *Ichthyosaura alpestris schuchensis* (**new combination**, not "*schouchensis*", as spelt by SOTIROPOULOS et al., 2007: 219), is currently available. Finally, the central European group (E) includes at least two subgroups. Despite morphological heterogeneity and a strong tendency to neoteny, the subgroup (E1) from Montenegro is genetically homogeneous (BRUIE & GUILLAUME, 1985; SOTIROPOULOS et al., 2007) and should better be recognized as a single subspecies, for which the nomen *Ichthyosaura alpestris montenegrina* (Radovanovic, 1951) (**new combination**) has priority. The other subgroup (E2), that straddles central Europe from Croatia to southern Romania and the Rodepe mountains in Bulgaria and Greece is possibly still heterogeneous. At this stage we

propose to recognize two subspecies in this group, *Ichthyosaura alpestris reiseri* (Werner, 1902) (**new combination**) from the Prokoško lake in Bosnia & Herzegovina, and *Ichthyosaura alpestris carpathica* (Dely, 1959) (**new combination**) for the other populations. Whereas the latter populations had until now not been separated from the hyponymous subspecies, the subspecies *reiseri* has long been recognized as distinct from the latter, and the use of a distinct nomen for it could be used as an argument for its conservation. Unfortunately, this subspecies appears to be extinct, following the introduction of trouts in the lake where it lived (DUBOIS, 1998b). Other populations of Alpine newts can be found on the Vranica mountain where this lake occurs, but they do not have the wide head so characteristic of *reiseri* (Michel Breuil, personal communication) and seem therefore to belong in the subspecies *carpathica*.

Large European newts

The genus *Triturus*, in the current narrow acceptance of the term (for the species *cristatus*, *marmoratus* and their relatives) has been the matter of numerous hybridization studies (see a subcomplete list of references in MACGREGOR et al., 1990: 339-340). Spontaneous hybridization between *cristatus* and *marmoratus* has long been known to exist in western France, where it results in newts of phenotypes "Blasi" and "Trouessarti", but without entailing a reciprocal gene flow between the two species. Gene flow appears also to be hampered, limited or asymmetrical in several other contact zones between taxa of this group, which has resulted in the recent years in the raising of several subspecies to species rank. We support these decisions. Of particular interest and significance is the case of the two taxa *cristatus* and *carniolensis*, long considered as subspecies of a single species *cristatus* but now considered distinct species. In the Geneva basin, which was inhabited by the former, the latter was introduced in recent times. Although in captivity these two forms hybridize without difficulty, in nature in this area they seldom did so, but they experienced drastic competition, and *carniolensis* progressively wiped *cristatus* out of this basin (ARNIZEN & THORPE, 1999). This is a good illustration of the mayron concept and of the fact that the existence of hybrids between two taxa does not necessarily mean that they are the same taxonomic species.

European smooth newts

In parallel with the situation in *Triturus*, and following largely the guidelines of HIGHTON (2000), we here elevate several former subspecies of the genus *Lissotriton* to species level.

The situation is rather simple in the subgenus *Mimus*. According to MARTINEZ-SOLANO et al. (2006), a significant geographic variation exists in *L. boscai*, with two major holophyletic groups in western and central Iberian peninsula, a south-western and a central-northern one. These authors, as well as MONFORI & LORENTI (2005) and RAFFAELLI (2007), suggested that these two groups deserve recognition as separate species, and we implement this change here, by resurrecting the nomen *Triton maltzani* Boettger, 1879 for the south-western species. *Lissotriton maltzani* (**new combination**) can be distinguished from *L. boscai* by its smaller size (55-80 mm vs. 75-100 mm) and by its dorsal coloration, which is paler than in *boscai*, especially in females, with less distinct dark spots.

The situation is more complex in the subgenus *Lissotriton*.

In the species *Lissotriton helveticus*, we here recognize the subspecies *alonsoi* and *punctillatus* following GARCÍA-PARÍS et al. (2004).

In the species *Lissotriton italicus*, RAGGHIANI et al. (1980) showed the existence of a chromosomal polymorphism distinguishing the northern and southern populations. RAGGHIANI & WAKE (1986) found allozyme polymorphism in the species but their data did not support specific status for the two groups (see also HIGHTON, 2000: 228). As the chromosomal differentiation between the two groups appears clear, we recognize them as subspecies. The nomen *Lissotriton italicus italicus* (Peracca, 1898) (**new onymorph**) applies to the southern subspecies and we propose to revalidate the nomen *Molge italica molisana* Altobello, 1926 for the northern one, as *Lissotriton italicus molisanus* (**new combination**). According to LANZA (1977), the series of symphoronts of this taxon was heterogeneous, being composed in part of *Lissotriton italicus* and of *Lissotriton meridionalis* specimens. As these specimens appear to have been lost, final stabilization of the status of this nomen will require the designation and description as neophoront of a *L. italicus* specimen from the Campobasso region (Molise, Italy).

The supraspecies *vulgaris* poses a difficult problem. RAXWORTHY (1990) recognized two species, *Lissotriton montandoni* and *Lissotriton vulgaris*, and reviewed the infraspecific taxonomy of the latter, with seven subspecies, known to hybridize in nature with each other and also with *montandoni*. He stated that "there can be no question of raising these taxonomic units to species rank based on the biological species concept" (p. 491). Recently however, BABIK et al. (2005) produced an interesting detailed phylogeographic analysis of this group, which in our opinion should entail taxonomic changes. They showed that the species *montandoni* was cladistically nested within the *vulgaris* group, rendering it paraphyletic. Several subgroups of *montandoni*, with different mitochondrial genomes, were uncovered by this analysis. It is likely that in some at least of these groups, several events of partial introgression of *vulgaris* mitochondrial genome took place in the last million years. Although important in some cases, the introgression of *vulgaris* mitochondrial alleles in *montandoni* does not seem to have significantly altered the morphology and ethology of the latter, which remains very homogeneous morphologically, in behaviour and habits throughout its range (JR, personal observations). The two species are readily distinguished in morphology and morphometrics, allozymes, chromosomes and courtship behaviour (see list of references in BABIK et al., 2005: 2488). Both species show a marked, although incomplete, behavioural sexual isolation (MICHÁJAK et al., 1998; MICHÁJAK & RAJČIŠKI, 1999). Therefore, just like in some populations of *Salamandra* mentioned above, *montandoni* and *vulgaris* clearly behave as separate entities in the field and should be recognized taxonomically as distinct mayrons. This is an example of the genetic homeostasy that characterizes mayrons, a fact that was stressed e.g. by MAYR (1975) with his concept of "cohesion of the genotype" and by TIMPIŦON (1989) with his "cohesion species concept". To put the things shortly and schematically, it appears that *montandoni* populations have "accepted" local and limited genetic introgressions from *vulgaris*, as far as these genetic changes did not significantly alter their overall phenotype and biology, i.e., as long as they allowed them to "remain *montandoni*".

The recognition of *montandoni* as a species distinct from *vulgaris* makes the latter paraphyletic and requires its splitting into several species. This is further justified by the existence of clear morphological differences between them and by the fact that gene flow

between them, where they meet, appears hampered and incomplete, with exchanges of portions of genomes which however do not obscure the recognition of the different entities (BABIK et al., 2005). This taxonomic decision is similar to what has been done recently in the genus *Triturus* (see above). On the basis of the data of BABIK et al. (2005), we suggest that the following six species should be recognized in this supraspecies: *Lissotritron graecus* (Wolterstorff, 1905) (**new combination**), *Lissotritron kossywi* (Freitag, 1955) (**new combination**), *Lissotritron lantzi* (Wolterstorff, 1914) (**new combination**), *Lissotritron meridionalis* (Boulenger, 1882) (**new combination**), *Lissotritron montandoni* (Boulenger, 1880) and *Lissotritron vulgaris* (Linnaeus, 1758). We provide below taxonoses for these species. Additionally, we recognize a subspecies *Lissotritron vulgaris ampelensis* (Fuhn, 1951) (**new combination**) in the species *vulgaris* (see RAFTIŃSKI et al., 2001, IFTIME & IFTIME, 2008). One of these nomina, *lantzi*, was first published (WOLTERSTORFF, 1914) as a quadrinomen (for a taxon below the rank subspecies) and was therefore unavailable in this original publication. Following a request by MERTENS & WERMUTH (1960a), this nomen was validated by the ICZN (RILLY & CHINA, 1962), a strange decision indeed, as this nomen had already been made available by NIKOLSKY (1918: 231), who had used it as a trinomial (*Molge vulgaris lantzi*) and had provided a diagnosis and a description. The nomen *ampelensis* was credited by MERTENS & WERMUTH (1960b: 32) to FUHN & FREITAG (1952), as a quadrinomial, but it was first used by FUHN (1951) as a trinomial, with a description, and is therefore available with this author and date.

RAXWORTHY (1990) recognized a subspecies *dubnaticus* (Kolombatović, 1907) which we consider as a synonym of *vulgaris* (see KRIZMANIĆ et al., 1997; BABIK et al., 2005). Several recent authors (e.g., RAXWORTHY, 1990; BABIK et al., 2005) recognized a subspecies *schmidlerorum*, which we also consider as a synonym of *vulgaris* (see OLGUN et al., 1999; THORN & RAFFAELLI, 2001; RAFFAELLI, 2007). Anyway, if it was to be recognized as a valid taxon, this should be under its original spelling *schmidleri* (RAXWORTHY, 1988). For reasons explained by DUBOIS (2007b), the spelling *schmidlerorum* is an invalid but available emendation that should be credited to RAXWORTHY (1990: 482). Finally, as for the nomen *tomasini* Wolterstorff, 1908, used by KRIZMANIĆ et al. (1997) and ČIROVIĆ et al. (2008) for a subspecies of *vulgaris*, this nomen is nomenclaturally unavailable, having been published as a quadrinomen and never validated by subsequent authors, and its validity is not supported by recent molecular and morphological studies (Spartak Litvinchuk, personal communication). If these populations from Montenegro had to be recognized as a subspecies of *graecus*, this would require the publication of a description and a nomen for them, as for the time being no available nomen exists for this taxon.

NEW, RESURRECTED AND EMENDED TAXA, NUCLEOSPECIFIC DESIGNATIONS AND NOMENCLATURAL COMMENTS

In this work, we strictly respect the rules of the *Code* regarding the number of ranks that can be used in zoological taxonomy. Therefore, as explained above, we only use two ranks in the genus-series (genus and subgenus) and four in the species-series (supraspecies, species, exerge and subspecies). In the family-series, although the *Code* allows for an undetermined number of ranks below family, for the purpose of our ergotaxonomy of the *Stomatopoda*

we only need the following four ranks: subfamily (nomen ending in *-INAE*), tribe (*-INI*), subtribe (*-INA*) and infratribe (*-ITA*).

For several of the new subgenera that we propose to recognize here, nomina are already available or can be made available through appropriate designation of nucleospecies. In order to clarify and stabilize their place in synonymies, we also designate below nucleospecies for all the nominal genera of *SALAMANDRIDAE* for which this had not been done previously, and we provide a few additional nomenclatural comments.

For each of the unnamed taxa that we first recognize here, we provide below a new nomen with its etymology and grammatical gender. To avoid the creation of long nomina like *Lyciasalamandra* or *Paramesotriton*, we use below the following simple roots for nomina designating some new taxa "*-triton*", from the generic nomen *Triton* Laurenti, 1768 (from the Greek *Triton*, son of Poseidon and God of the sea), for genera of "newts"; and "*-andra*", the last five letters of the nomen *Salamandra* Laurenti, 1768 (from the Greek *salamandra*, "salamander"), for genera of "true salamanders". Other roots used in a few other cases are explained where appropriate.

In the section below we only discuss the family-series and genus-series taxa that are created or modified (emended) here, but not those which are used here in the same sense and with the same content as in the recent literature, nor those of the species-series, for which we provide no new nomen. Taxa are presented below by alphabetical order of their nomina at all levels. We do not provide in the text below the lists of the species included in each of the new or emended taxa defined below, as they appear in the complete new ergotaxonomy of the family *SALAMANDRIDAE* Goldfuss, 1820 which is given in table 5.

For each taxon discussed below, we provide short definitions or taxognoses, in the forms of an *entevognosis*, a *diagnosis* (in one of the tables 1-4) and an *idivognosis* (see above for explanations).

The entevognoses provide phylogenetic definitions of the taxa as holophyletic groups including and excluding a few chosen species.

The characters used in the diagnoses were described in TWITTY (1964), MICHAM (1967*a-b*, 1968), SALTIN (1967), THORN (1969), MORESCALCHI (1975), NUSSBAUM & BRODIE (1981*a-c*), PICIO & RAJINSKI (1985), TITUS & LARSON (1995), SPARRIBOOM et al. (2000), CHAN et al. (2001), FRIE et al. (2006), WISROCK et al. (2006) and RAFFAELLI (2007). We also use some of the characters provided in the original descriptions of some taxa, as well as personal observations and those of several colleagues and friends (see *Acknowledgements*).

Size in the diagnoses is given as TL (total length in millimetres, from tip of snout to tip of tail). For the purpose of these diagnoses, we recognize four different breeding behaviours in the *SALAMANDRIDAE* (SALTIN, 1967, TITUS & LARSON, 1995): nuptial dance, type I amplexus or "caudal capture", type II amplexus or "ventral capture", type III amplexus or "dorsal capture". Two distinct modes of nuptial dance can also be distinguished: a "simple" one in which the male and female follow each other, and an "elaborated" one, in which the male executes caudal movements. Three kinds of reproduction modes exist in the genus *Salamandra*, which, according to the terminology of DUBOIS (2004*b*) are here designated as follows: *ovoviviparity lecithotroph*, for embryos developing within the eggs kept in the female genital tract, feeding on the vitelline reserves of the eggs, *viviparity adelphotroph* for embryos that

develop within the female genital tract, feeding on their brothers and sisters; and *viviparity matrotroph* for embryos that develop within the female genital tract, feeding on secretions of the latter. Another, rather unusual, character, that we use in taxognoses, is the adaptability of the species to terrarium, for which, based on the personal experiences of one of us (JR) and of several other breeders (personal communications), we recognize two categories: *high adaptability in terrarium* (HAT), for species that can be kept for several years in captivity under various conditions of temperature, humidity and food offer, in terraria where they can develop complete breeding behaviour and give birth to offspring, sometimes repeatedly, and *low adaptability in terrarium* (LAT), for species that do not easily reproduce in captivity and are reluctant to variability for conditions of temperature, humidity, food offer and general husbandry; in the last case, animals must be kept under strict conditions of captivity which have to be determined on a permanent basis. This criterion expresses in a synthetic way several ethological, physiological and more generally biological characteristics and limitations of the organisms (requirements and constraints regarding temperature, humidity, space, shelter, etc.), that have not been analysed in detail yet although this would certainly be possible.

Beside entexognoses and diagnoses, we provide short idiognoses for most of the taxa, which give a few major characters in a non-comparative way. All these idiognoses follow the same plan (1) Size (range or maximum known for each taxon) (2) Morphology (3) Coloration. (4) Sex dimorphism. (5) Behaviour. (6) Adaptability in terrarium. (7) Distribution. (8) Miscellanea

The higher nomenclature of the URODELA used below is that of DUBOIS (2005c). If a class-series taxon, e.g. of rank phalanx (see DUBOIS, 2006a) is to be recognized for the group including the families *AMBYSTOMATIDAE* and *SALAMANDRIDAE*, its valid nomen is *MUTABILIA* Merrem, 1820, a senior synonym of *TREPITOBRANCHIA* Frost et al., 2006 (see DUBOIS & OHLER, 2009).

Classis *AMPHIBIA* De Blainville, 1816

Subclassis *NFOBATRACHI* Sarasin & Sarasin, 1890

Superordo *BATRACHIA* Brongniart, 1800

Ordo *URODELA* Dumeril, 1806

Phalanx *MUTABILIA* Merrem, 1820

Family *SALAMANDRIDAE* Goldfuss, 1820

Subfamilia *PLEURODELINAE* Tschudi, 1838

Nucleogenus. – *Pleurodeles* Michahelles, 1830: 195, by implicit etymological designation

Entexognosis. The most inclusive holophyletic taxon including the species *Pleurodeles waltli* (Michahelles, 1830) and excluding the species *Salamandra salamandra* (Linnaeus, 1758) and *Salamandrina perspicillata* (Savi, 1821).

Diagnosis. – See table 1

Table 1. — Diagnostic comparisons among five groups composed of three parordinate taxa as recognized here

Superordinate taxon	Familia SALAMANDRIDAE Goldfuss, 1820		
Parordinate taxa	Subfamilia PLEURODELIINAE Tschudi, 1838	Subfamilia SALAMANDRINAE Goldfuss, 1820	Subfamilia SALAMANDRINAE Fitzinger, 1843
Frontosquamosal arch	Present	Absent	Present
Promaxillary bones	Paired or fused	Paired	Paired
Apical chromosome number	24 or 22	24	24
Dorsal lordose	Present	Absent	Present
Breeding behaviour	Nuptial dance (simple or elaborated), or type I, II or III amplexus	Type II amplexus	Nuptial dance (simple)
Superordinate taxon	Subtribus MOGISTA Gray, 1850		
Parordinate taxa	Infratribus CYNOPITA nov	Infratribus ET PROCTIPA nov	Infratribus MOGISTA Gray, 1850
Skia	Boxlike, with flattened dorsal surface	Very flattened	Not flattened (except in <i>Colostrotus</i>), narrow, sometimes box-like
Frontosquamosal arch	Complete	Nearly absent	Absent, incomplete or complete
Limbs	Present	Absent or very reduced	Present
Ventral coloration	Always red or reddish	Never red or reddish	Never fully red
Breeding behaviour	Nuptial dance (elaborated)	Type I amplexus	Type I amplexus or nuptial dance (elaborated)
Adaptability to aquatic life	HAT or LAT	LAT	HAT
Superordinate taxon	Subgenus LIXOTRITON (<i>Lixotriton</i>) Bell, 1839		
Parordinate taxa	Supraspecies <i>helveticus</i> (Razoumowsky, 1789)	Supraspecies <i>usaticus</i> (Peracca, 1878)	Supraspecies <i>vulgaris</i> (Linnaeus, 1758)
Size	TL 65-92 mm	TL 55-80 mm	TL 70-111 mm
Dorsal crest in breeding male	Present	Absent	Present
Palm on toes in breeding male	Present	Absent	Present
Tail fin in breeding male	Present	Present	Present or absent
Spots on venter of male	Absent	Present	Present or absent
Horizontal black line through eye	Present	Absent	Present
Whip on male male genitalia	Well-developed	Attenuated	Well-developed
Adaptability to aquatic life	HAT	LAT	HAT or LAT
Superordinate taxon	Subgenus SALAMANDRA (<i>Salamandra</i>) Laurenti, 1768		
Parordinate taxa	Species <i>Salamandra atra</i> (Müller & Hellmich, 1935)	Species <i>Salamandra atra</i> (<i>Salamandra</i>) Joger & Steinfuriz, 1994	Species <i>Salamandra atra</i> (<i>Salamandra</i>) (Linnaeus, 1758)
Size	TL up to 130 mm	TL up to 188 mm	TL 110-280 mm
Habitus	Slender	Slender	Slender to stout
Head	Small narrow	Medium rather wide	Small to large narrow to wide
Snout	Pointed	Very pointed	Rounded to pointed
Yellow spots or bands	Very few spots	Many large spots	5 spots or bands
Red (or orange) color	Absent	Absent	Present
Reproduction mode	Oviparity lecithotroph	Oviparity lecithotroph	Oviparity lecithotroph or viviparity auxiparous
Duration of free larval development	Long	Short	Short to long, or absent
Altitudinal distribution	High	Medium	Low to high
Adaptability to terrain	LAT	LAT	LAT to HAT
Superordinate taxon	Species <i>Salamandra atra</i> (<i>Salamandra</i>) (Linnaeus, 1758)		
Parordinate taxa	Esophage <i>erythraea</i> (Malkmus, 1983)	Esophage <i>fastuosa</i> (Schreibler, 1912)	Esophage <i>salmonida</i> (Linnaeus, 1758)
Size	TL up to 780 mm	TL 100-160 mm	TL 200-280 mm
Head	Stout	Slender	Stout
Head	Narrow	Narrow	Wide
Spots or lines	Spots	Lines	Lines or spots
Yellow colour	N or ochraceous	Live save	Rarely extensive
Red colour	Always	Rare	Rare
Orange colour	Never	Never	Rare
Reproduction mode	Oviparity lecithotroph	Viviparity auxiparous (viviparity lecithotroph in <i>gobulata</i>)	Oviparity lecithotroph
Adaptability to terrain	LAT	HAT	LAT

Tribus *MOLGINI* Gray, 1950

Nucleogenus. – *Molge* Merrem, 1820, 166, by original specific monophory.

Entexognosis. The most inclusive holophyletic taxon including the species *Pleurodeles waltl* (Michahelles, 1830) and excluding the species *Triturus cristatus* (Laurenti, 1768).

Diagnosis. – See table 2.

Subtribus *MOLGINA* Gray, 1950

Nucleogenus. *Molge* Merrem, 1820, 166, by implicit etymological designation.

Entexognosis. The most inclusive holophyletic taxon including the species *Triturus cristatus* (Laurenti, 1768) and excluding the species *Taricha torosa* (Rathke, 1833)

Diagnosis. – See table 2.

Idiognosis. – (1) TL 55-250 mm. (2) Habitus slender to stout. (3) Dorsal and ventral colorations usually very contrasted. (4) Sex dimorphism strong. Dorsal crest present or absent. (5) Breeding habitat lentic or lotic. Type I amplexus or nuptial dance (elaborated) (6) HAT or LAT. (7) Palearctic.

Infratribus *CYNOPTA* nov.

Nucleogenus. *Cynops* Tschudi, 1838, 59, by present designation

Entexognosis. The most inclusive holophyletic taxon including the species *Cynops pyrrhogaster* (Boie, 1826) and excluding the species *Euproctus platycephalus* (Gravenhorst, 1829) and *Triturus cristatus* (Laurenti, 1768)

Diagnosis. – See table 1.

Idiognosis. (1) TL 70-250 mm. (2) Habitus usually stout. Head boxlike. Trunk usually quadrangular. Skin smooth to very granular. (3) Dorsal coloration usually dull. Ventral coloration bright, with red, reddish or orange spots. (4) Sex dimorphism strong. (5) Mainly aquatic, in lentic or lotic habitat. Nuptial dance (elaborated). (6) HAT or LAT. (7) Eastern Palearctic and northern Oriental regions. (8) Distal tarsal 4 and 5 fused

Genus *Cynops* Tschudi, 1838

Nucleospecies. *Salamandra subcristata* Temminck and Schlegel, 1838, 117 (neonym for *Molge pyrrhogaster* Boie, 1826: 215), by original specific monophory

Etymology. From the Greek *kuon*, genitive of *kuon* ("dog") and *opsis* ("aspect, appearance"). This nomen clearly refers to the fact that the head of males of *Cynops pyrrhogaster*, the species used for the description of the genus, looks like a dog's head, because of its very sharp canthus rostralis and of the presence of an excrescence at the rear of

the head. These two characters however are absent in *ensicauda*, the other species of this genus.

Grammatical gender. – Masculine.

Entoxognosis. The most inclusive holophyletic taxon including the species *Cynops pyrrhogaster* (Boie, 1826) and excluding the species *Hypselotriton wolterstorffi* (Boulenger, 1905), *Pachytriton brevipes* (Sauvage, 1877), *Laotriton laoensis* (Stuart & Papenfuss, 2002) (**new combination**) and *Paramesotriton deloustali* (Bourret, 1934).

Diagnosis. – See table 3.

Idiognosis. (1) Medium (TL 120-150 mm) (2) Habitus stout. Trunk quadrangular. Skin very granular. (3) Dorsal coloration usually dull. Ventral coloration very bright, with red, reddish or orange spots. (4) Sex dimorphism strong, male smaller than female. (5) Mainly aquatic, in lentic habitat. (6) HAT. (7) Japan. (8) Nasals broadly in contact, sharp vertebral ridge.

Genus *Hypselotriton* Wolterstorff, 1934

Nucleospecies. *Molge wolterstorffi* Boulenger, 1905: 277, by original designation.

Etymology. From the Greek *hupselos* ("high") and the generic nomen *Triton* Laurenti, 1768.

Grammatical gender. – Masculine.

Entoxognosis. The most inclusive holophyletic taxon including the species *Hypselotriton wolterstorffi* (Boulenger, 1905) and excluding the species *Cynops pyrrhogaster* (Boie, 1826), *Pachytriton brevipes* (Sauvage, 1877), *Laotriton laoensis* (Stuart & Papenfuss, 2002) and *Paramesotriton deloustali* (Bourret, 1934).

Diagnosis. – See table 3.

Idiognosis. (1) TL 70-160 mm. (2) Habitus stout. Trunk almost quadrangular. Skin smooth or slightly granular. (3) Dorsal coloration dull. Ventral coloration very bright, with red, reddish or orange spots. (4) Sex dimorphism strong, male very small. (5) Mainly aquatic, in lentic habitat. (6) HAT or LAT. (7) China. (8) Nasals separated or in slight contact, weak vertebral ridge.

Subgenus *Hypselotriton* Wolterstorff, 1934

Nucleospecies, etymology and grammatical gender. See above under genus *Hypselotriton*.

Entoxognosis. The most inclusive holophyletic taxon including the species *Hypselotriton wolterstorffi* (Boulenger, 1905) and excluding the species *Hypselotriton grandulosus* (Chang, 1933).

Diagnosis. – See table 2.

Idiognosis. (1) TL 70-160 mm. (2) Habitus stout. Trunk almost quadrangular. Parotoids weakly developed. Skin smooth. (3) Dorsal coloration mostly dull. Ventral coloration very

Table 2 Diagnostic comparisons among thirteen groups composed of two parordinate taxa as recognized here

Superordinate taxon	Subfamily <i>PLEUKODELINAE</i> Tschudi, 1838	
Parordinate taxa	Tribus <i>MOLGINI</i> Gray, 1850	Tribus <i>PLEUKODELINI</i> Tschudi, 1838
Premaxillary bones	Fused	Paired
Skin	Smooth or slightly granular	Very granular
Breeding behaviour	Type I or type III amplexus, or nuptial dance (elaborated)	Nuptial dance (simple) or type II amplexus
Superordinate taxon	Tribus <i>MOLGINI</i> Gray, 1850	
Parordinate taxa	Subtribus <i>MOLGINA</i> Gray, 1850	Subtribus <i>TARICHINA</i> nov.
Diploid chromosome number	24	22
Dorsal crest in breeding male	Present or absent	Absent
Breeding behaviour	Nuptial dance (elaborated) or type I amplexus	Type III amplexus
Adaptability in terrarium	HAT or LAT	HAT
Superordinate taxon	Genus <i>Hypselotriton</i> Wolterstorff, 1934	
Parordinate taxa	Subgenus <i>Hypselotriton</i> Wolterstorff, 1934	Subgenus <i>Pingua</i> Chang, 1935
Frontal process of premaxillary	Long	Short
Parotoid glands	Weakly developed	Well developed
Tubercles on external side of hands and feet	Present	Absent
Skin	Very finely granular, nearly smooth	Slightly to very granular
Adaptability in terrarium	LAT	HAT or unknown
Altitudinal distribution	High altitude (1800-2600 m)	Low altitude (0-1000 m)
Superordinate taxon	Genus <i>Paramesotriton</i> Chang, 1935	
Parordinate taxa	Subgenus <i>Allomesotriton</i> Freytag, 1983	Subgenus <i>Paramesotriton</i> Chang, 1935
Habitus	Slender	Robust
Skull	Long and narrow	Short and broad
Frontosquamosal	Incomplete	Complete
Epibranchials	Moderately stout and bony	Very stout and bony
Dorsal callus	Clear	Dark
Habitat	Very aquatic, flying water	Slightly aquatic, mostly flying water
Superordinate taxon	Genus <i>Lissotriton</i> Bell, 1839	
Parordinate taxa	Subgenus <i>Lissotriton</i> Bell, 1839	Subgenus <i>Meunus</i> nov.
Frontosquamosal arch	Weak, sometimes entirely ligamentary	Very strong
Perianal cloaca	Slightly enlarged but not prominent	Cone-shaped, very prominent
Whip and wave during male nuptial dance	Present (reduced in <i>L. italicus</i>)	Absent
Habitat	Mainly terrestrial, aquatic only during breeding	Very aquatic
Adaptability in terrarium	HAT	LAT
Superordinate taxon	Genus <i>Neurergus</i> Cope, 1862	
Parordinate taxa	Subgenus <i>Mavericus</i> nov.	Subgenus <i>Neurergus</i> Cope, 1862
Ventral coloration	Dark, with median longitudinal orange band	Bright
Colour of sides of adult breeding male	Silver-blue	Not silver-blue
Superordinate taxon	Genus <i>Triturus</i> Rafinesque, 1815	
Parordinate taxa	Subgenus <i>Pyronica</i> Gray, 1858	Subgenus <i>Triturus</i> Rafinesque, 1815
Dorsal coloration	Green	Black
Ventral coloration	Black and white	Yellow or orange with black spots
Dorsal crest of breeding male	Undulating	Denticulated
Habitat	Highly terrestrial	Rather aquatic
Adaptability in terrarium	LAT	HAT
Superordinate taxon	Genus <i>Notophthalmus</i> Rafinesque, 1820	
Parordinate taxa	Subgenus <i>Notophthalmus</i> Rafinesque, 1820	Subgenus <i>Rafinus</i> nov.
Spots on dorsum and venter	Small	Large
Male secondary sex character	Transverse black horny ridges on thighs	No transverse black horny ridges on thighs
IB stage	Present	Absent
Necklers	Present	Absent
Habitat	Very aquatic	Mainly terrestrial

Table 2 – (continued)

Superordinate taxon	Genus <i>Taricha</i> Gray, 1850	
Parordinate taxa	Subgenus <i>Taricha</i> Gray, 1850	Subgenus <i>Twaitya</i> nov.
Iris	Yellow or partially yellow	Black
Ventral coloration	Yellow to orange	Red
Egg deposition	Singly or in clumps of 7-39 eggs	Clumps of 6-16 eggs
Habitat	Standing or mildly flowing water	Flowing water
Superordinate taxon	Genus <i>Tylostrotion</i> Anderson, 1871	
Parordinate taxa	Subgenus <i>Tylostrotion</i> Anderson, 1871	Subgenus <i>Yaotriton</i> nov.
Size	TL up to 230 mm	TL 120-160 mm
Dorsal coloration	Black with colored spots	Mainly black
Deposition site of eggs	In water	On land or in contact with water
Habitat	Partially aquatic	Terrestrial
Adaptability in terrarium	HAT	LAT
Superordinate taxon	Subfamily SALAMANDRINAE Goldfuss, 1820	
Parordinate taxa	Tribus <i>CHIOGLOSSINI</i> nov.	Tribus <i>SALAMANDRINI</i> Goldfuss, 1820
Size	TL 150-200 mm	TL 110-324 mm
Habitus	Slender	Stout
Precapillaries	Paired with short posterior prolongations	Paired with long posterior prolongations
Nails	Large in contact with each other	Small, separate from each other
Reproduction mode	Oviparity	Ovoviviparity or viviparity
Mode of life	Mainly aquatic	Terrestrial
Adaptability in terrarium	LAT	HAT
Superordinate taxon	Subgenus <i>Aligandra</i> nov.	
Parordinate taxa	Species <i>Salamandra algira</i> Bedriaga, 1883	Species <i>Salamandra tangitana</i> Donaire Barroso & Bogeris, 2003
Size	TL up to 230 mm	TL up to 210 mm
Habitus	Slender	Stout
Glands on dorsum of breeding male	Absent	Present
Yellow spots	Small spots, often regular	Very small spots, irregular, sometimes absent
Red colour	Present	Absent
Reproduction mode	Ovoviviparity lecithotroph	Viviparity adelphotroph
Adaptability in terrarium	LAT	HAT
Superordinate taxon	Subgenus <i>Alpandra</i> nov.	
Parordinate taxa	Species <i>Salamandra atra</i> Laurenti, 1768	Species <i>Salamandra aurarae</i> Trevisan, 1982
Head	Narrow	Moderately narrow
Dorsal coloration	Black, sometimes very few yellow spots	Black yellow bands
Distribution range	Large	Narrow
Adaptability in terrarium	LAT	HAT

bright, red (4) Sex dimorphism strong, male very small. (5) Fully aquatic, in lentic habitat. (6) LAT, with a narrow gradient of temperature (12-25°C). (7) Western China (8) Tubercles on the external side of hands and feet.

Subgenus *Pingia* Chang, 1935

Nucleospecies. *Pachytriton granulatus* Chang, 1933, 320, by original specific monophory

Etymology From the patronym of Prof Chih Ping (1886-1965), then director of the biological laboratory of Nankin (CHANG, 1936, 3, 103).

Grammatical gender. Feminine

Entoxognosis – The most inclusive holophyletic taxon including the species *Hypselotriton granulatus* (Chang, 1933) and excluding the species *Hypselotriton wolterstorffi* (Boulenger, 1905).

Table 3. Diagnostic comparisons among a group composed of five parordinate taxa as recognized here

Superordinate taxon	Infratribus <i>CYNOPITA</i> nov.				
Parordinate taxa	Genus <i>Cynops</i> Tschudi, 1838	Genus <i>Hypselotriton</i> Wolterstorff, 1934	Genus <i>Laotriton</i> nov.	Genus <i>Pachytriton</i> Boulenger, 1878	Genus <i>Paramesotriton</i> Chang, 1935
Size	TL 130-50 mm	TL 80-60 mm	TL 180-250 mm	TL 160-200 mm	TL 130-200 mm
Snout	Long and slim	Thin and flat	Long and arc. flat	Wide and flat	Long and wide
Number of vertebrae	13	13	12	12-(13)	(11)-12
Parotoids	Very prominent	Slightly prominent	Very prominent	Prominent	Prominent
Tongue pad	Long	Long	Reduced, without free posterior margin	Reduced	Long
Skin	Very granular without distinct warts	Smooth to very granular without distinct warts	Very granular with distinct warts	Smooth	Usually very granular with distinct warts
Vertebral ridge	Prominent	Almost absent	Prominent	Absent	Prominent
Lateral ridges	Absent	Absent	Present	Absent	Present
Dorsal coloration	Usually dull	Dull	Bright	Dull	Dull
Adaptability in terrarium	HAT	HAT or LAT	LAT	LAT	LAT

Diagnosis. – See table 2.

Idiagnosis. (1) TL 70-100 mm. (2) Habitus stout. Trunk almost quadrangular. Parotoids well developed. Skin slightly to very granular. (3) Dorsal coloration dull. Ventral coloration very bright, red. (4) Sex dimorphism strong, male small. (5) Mainly aquatic, in lentic habitat. (6) HAT, with tolerance of a large gradient of temperature (5-25°C); adaptability in captivity of *Hypselotriton granulatus* unknown. (7) Eastern China. (8) No tubercles on the external side of hands and feet.

Genus *Laotriton* nov.

Nucleospecies *Paramesotriton laotensis* Stuart & Papenfuss, 2002. 145, by present designation.

Etymology From the Laotian *Laos* (name of the country) and the generic nomen *Triton* Laurenti, 1768.

Grammatical gender. – Masculine.

Entexognosis The most inclusive holophyletic taxon including the species *Laotriton laotensis* (Stuart & Papenfuss, 2002) and excluding the species *Cynops pyrrhogaster* (Boie, 1826), *Hypselotriton wolterstorffi* (Boulenger, 1905), *Pachytriton brevipes* (Sauvage, 1876) and *Paramesotriton deloustali* (Bourret, 1934).

Diagnosis. – See table 3.

Idiagnosis (1) TL 180-250 mm. (2) Habitus very stout. Snout truncated, head large and very flat. Tail of female long. Skin warty, with many tubercles on upper side of trunk. (3) Dorsal and ventral coloration bright. (4) Sex dimorphism moderate. (5) Completely aquatic, in lotic habitat. (6) LAT, with tolerance of a narrow gradient of temperature (16-25°C). (7) Laos.

Genus **Paramesotriton** Chang, 1935

Nucleospecies. *Mesotriton deloustali* Bourret, 1934, 83, by original specific monophory under *Mesotriton* Bourret, 1934: 83 (nec *Mesotriton* Bolkay, 1927: 64).

Etymology. From the Greek *para* ("near, beside"), *mesos* ("in the middle of") and the generic nomen *Triton* Laurenti, 1768.

Grammatical gender. – Masculine.

Entexognosis. The most inclusive holophyletic taxon including the species *Paramesotriton deloustali* (Bourret, 1934) and excluding the species *Cynops pyrrhogaster* (Boie, 1826), *Hypselotriton wolterstorffi* (Boulenger, 1905), *Laotriton laoensis* (Stuart & Papenfuss, 2002) and *Pachytriton brevipes* (Sauvage, 1876).

Diagnosis. – See table 3.

Idiognosis. (1) TL 130-200 mm. (2) Habitus slender to very stout. Snout truncated, head narrow to large. Tail of female medium. Skin smooth to warty. (3) Dorsal coloration usually dull, ventral coloration bright. (4) Sex dimorphism usually moderate. (5) Usually aquatic, in lotic habitat. (6) LAT, with tolerance of a rather large gradient of temperature (10-25°C). (7) China, Vietnam.

Subgenus **Allomesotriton** Freytag, 1983

Nucleospecies. *Trituroides caudopunctatus* Liu & Hu in HU, DIAO & LIU, 1973, 151, by original designation.

Etymology. From the Greek *allos* ("different, strange"), *mesos* ("in the middle of") and the generic nomen *Triton* Laurenti, 1768.

Grammatical gender. – Masculine.

Entexognosis. The most inclusive holophyletic taxon including the species *Paramesotriton caudopunctatus* (Liu & Hu in HU, DIAO & LIU, 1973) and excluding the species *Paramesotriton deloustali* (Bourret, 1934).

Diagnosis. – See table 2.

Idiognosis. (1) TL 150 mm. (2) Habitus slender. Snout truncated, head narrow. Skin nearly smooth. (3) Dorsal coloration light brown, ventral coloration bright. (4) Sex dimorphism rather strong. (5) Fully aquatic, in lotic habitat. (6) LAT, with tolerance of a narrow gradient of temperature (10-20°C). (7) Southern China.

Subgenus **Paramesotriton** Chang, 1935

Nucleospecies, etymology and grammatical gender. – See above under genus *Paramesotriton*.

Entexognosis. The most inclusive holophyletic taxon including the species *Paramesotriton deloustali* (Bourret, 1934) and excluding the species *Paramesotriton caudopunctatus* (Liu & Hu in HU, DIAO & LIU, 1973).

Diagnosis. – See table 2.

Idiognosis (1) TL 130-200 mm. (2) Habitus very stout. Snout truncated, head large. Skin warty, with many tubercles on upper side of trunk. (3) Dorsal coloration dull, ventral coloration bright. (4) Sex dimorphism moderate. (5) Usually aquatic, in lotic habitat. (6) LAT, with tolerance of a rather large gradient of temperature (10-25°C). (7) China, Vietnam.

Infratribus *EUPROCTITA* nov

Nucleogenus *Euproctus* Gene, 1839: 281, by present designation

Entexognosis. – The most inclusive holophyletic taxon including the species *Euproctus platycephalus* (Gravenhorst, 1829) and excluding the species *Cynops pyrrhogaster* (Boie, 1826) and *Triturus cristatus* (Laurenti, 1768).

Diagnosis. – See table 1.

Idiognosis. (1) FL 130-140 mm. (2) Habitus slender. Head and trunk flattened. Skin smooth. (3) Dorsal coloration usually dull. Ventral coloration never red or orange. (4) Sex dimorphism moderate, spur on the male hind limbs. (5) Mainly aquatic, in lotic habitat. Type I amplexus. Parental care in one of two species. (6) LAT, with tolerance of a narrow gradient of temperature (5-15°C). (7) Western Palearctic (Corsica, Sardinia).

Infratribus *MOLGITA* Gray, 1950

Nucleogenus. *Molge* Merrem, 1820: 166, by implicit etymological designation

Entexognosis. The most inclusive holophyletic taxon including the species *Triturus cristatus* (Laurenti, 1768) and excluding the species *Cynops pyrrhogaster* (Boie, 1826) and *Euproctus platycephalus* (Gravenhorst, 1829).

Diagnosis. – See table 1.

Idiognosis. (1) TL 55-180 mm. (2) Habitus usually stout. Head usually long and slender. Trunk rounded or slightly flattened. Skin smooth or slightly granular. (3) Dorsal and ventral coloration usually bright. Ventral coloration rarely red or orange. (4) Sex dimorphism strong. (5) Aquatic during breeding period, in lentic or lotic habitat. No amplexus, except in *Calotriton*. (6) Usually HAT. (7) Western Palearctic.

Genus *Ichthyosaura* Sonnini & Latreille, 1801

Nucleospecies. – *Proteus tritonius* Laurenti, 1768: 37, by original specific monophory

Comment. As rightly pointed out by SCHMIDHEER (2004: 22), and acknowledged by SPIVAK-BROECK & CROCHET (2007), LESURE (2008) and BOUËR et al. (2008), the nomen *Ichthyosaura* Sonnini & Latreille, 1801 is the first available one for the genus including the nominal species *Triton alpestris* Laurenti, 1768, and it has priority over *Mesotriton* Bolkay, 1927 (nucleospecies, *Triton alpestris* Laurenti, 1768) by subsequent designation of THORN, 1969: 191. The

synonymy between the nominal species *Proteus tritonius* Laurenti, 1768 and *Triton alpestris* Laurenti, 1768 is beyond doubt, not only because the description and figure of the former fully fits a larva of newt, not of salamander, but also because both are based on specimens from the same onymotope, a small lake north-east of the top of the mount Otscher (1893 m) in Niederösterreich (Lower Austria). A larva of *alpestris* from this locality should be designated as neotype for the specific nomen *tritonius* to stabilize definitively the status of the latter. Another newt species could possibly occur in this locality, *Lissotriton vulgaris*, but this would have to be demonstrated by new field data. No specimen of newt from this mountain is to be found in the national collections of the Naturhistorisches Museum Wien (Heinz Grillitsch, personal communication). If a larva of *vulgaris* was designated as neotype of *tritonius*, *Ichthyosaura* would have to replace *Lissotriton* as the valid nomen for the genus of smooth newts.

The nomen *Ichthyosaura* should be credited to SONNINI & LATREILLE (1801*b*), not to "Latreille in SONNINI & LATREILLE (1801*b*)". In the introduction of the first volume of this 4-volume work, SONNINI & LATREILLE (1801*a*) stated that Latreille had written the parts dealing with the tortoises, lizards, frogs, toads, tree-frogs and snakes, whereas Sonnini had written the part dealing with the salamanders and the introduction. But they did not state who had written the part entitled "Eclaircissements [sic] et additions" that appeared in pages 239-313 of the fourth volume, where the new generic nomen *Ichthyosaura* was proposed (p. 310), so this part, and the new nomen, must simply be credited to SONNINI & LATREILLE (1801*b*).

Another synonym of *Ichthyosaura* and *Mesotriton* overlooked by all authors until now is *Hemitriton* Dugès, 1852: 255. *ASW* states that the nucleospecies of this nomen has never been designated, but nevertheless places it in the synonymy of *Euproctus* Gene, 1839, which is both contradictory and twice erroneous. DUGÈS (1852) included six nominal species in his new genus *Hemitriton*: *Triton alpestris* Laurenti, 1768 from the Alps, *Hemitriton asper* Dugès, 1852 from the Pyrenees and five other nominal species from the latter mountains which he finally himself considered (DUGÈS, 1852: 267) as synonyms of the latter. By placing this nominal genus in the synonymy of *Euproctus*, *ASW* seems to imply that the genus was meant for the Pyrenean species, but then, if it was the case, the nomen should be placed in the synonymy of *Calotriton* Gray, 1858, not of *Euproctus*. But this is also wrong for ignoring a subsequent nucleospecies designation for this genus. Twenty years after the original description, FATIO (1872: 516) clearly designated *Triton alpestris* as the "type" of this taxon (which he treated as a subgenus of *Triton*) (**valid nucleospecies designation**), and expressed doubts (FATIO 1872: 540) about the placement of the Pyrenean species in this genus. The nomen *Hemitriton* Dugès, 1852 is therefore a junior synonym of *Ichthyosaura* Sonnini & Latreille, 1801 (**new synonymy**). It is preoccupied in zoology by *Hemitriton* Van der Hoeven, 1833: 305, a nomen that *ASW* qualifies as "substitute name for *Hypochthon Merrem*, *Menobranchus Harlan* and *Siredon Wagler*" and places in the synonymy of *Proteus* Laurenti, 1768. *Acetatus* Rafinesque, 1819 and *Ambystoma* Eschsch, 1838. This is nomenclaturally impossible because, as stated above, a given nomen cannot be synonym for several distinct nomina and cannot appear in several synonymies. In fact, VAN DER HOEVEN (1833: 305) proposed his nomen *Hemitriton* for a *new genus* including three distinct subgenera, for which he used the nomina *Hypochthon* Merrem, 1820 (with two nominal species), *Menobranchus* Harlan, 1825 (with one nominal species) and *Siredon* Wagler, 1830 (with one nominal species). We hereby designate the nominal species *Proteus anguinus* Laurenti, 1768: 31 as nucleospecies of *Hemitriton* Van der Hoeven, 1833.

(**new nucleospecies designation**), which will therefore now have to stand in the synonymy of *Proteus Laurenti*, 1768 as an objective synonym (**new synonym**).

Genus *Lissotriton* Bell, 1839
Subgenus *Lissotriton* Bell, 1839

Nucleospecies. – *Salamandra punctata* Latreille, 1800, by subsequent designation of FITZINGER, 1843: 34

Etymology. – From the Greek *lyssos* (“smooth”) and the generic nomen *Triton* Laurenti, 1768

Grammatical gender. – Masculine

Entexognosis The most inclusive holophyletic taxon including the species *Lissotriton vulgaris* (Linnaeus, 1758) and excluding the species *Lissotriton boscai* (Lataste in Blanchard, 1879).

Diagnosis. See table 2. See also table 1 for the diagnostic comparisons of the supra species *helveticus*, *italicus* and *vulgaris*, and table 4 for those of the six species of the latter supraspecies.

Idiognosis (1) TL 55-120 mm. (2) Habitus stout. Head elongated. (3) Ventral coloration variable, often with big black spots. Horizontal black line through eye usually present. (4) Sex dimorphism strong. Male usually much smaller than female, usually with crest on back. Female cloaca not conic. (5) Mostly terrestrial, breeding in lentic habitat. Whip and wave during nuptial dance of male, sometimes attenuated. (6) HAT. (7) Europe to Siberia.

Subgenus *Meinus* nov.

Nucleospecies *Pelonectes boscai* Lataste in Blanchard, 1879: 276, by present designation

Etymology Unknown. Nomen borrowed from RAFINESQUE (1815-78) who published it as a synonym. We have no clue on the meaning intended by its author for this nomen, except that it bears some resemblance to the Latin term *minus*, meaning “less”.

Grammatical gender. – Masculine.

Entexognosis The most inclusive holophyletic taxon including the species *Lissotriton boscai* (Lataste in Blanchard, 1879) and excluding the species *Lissotriton vulgaris* (Linnaeus, 1758)

Diagnosis – See table 2.

Idiognosis (1) TL 70-100 mm. (2) Habitus stout. Head elongated. (3) Ventral coloration reddish-orange with black spots. Horizontal black line through eye absent. (4) Sex dimorphism strong. Male much smaller than female, without crest on the back. Female cloaca conic. (5) Very aquatic, in lentic habitat. No whip and wave during nuptial dance of male. (6) LAT. (7) Western Iberian Peninsula.

Comments The case of the synonym “*Meinus*” Rafinesque, 1815 was briefly presented above. This nomen has never been “validated” since its creation, and is still unpreoccupied in

zoological nomenclature. As we need a nomen for the subgenus of *Lissostriton* including the species *Lissostriton boscai* (see above), and as this nomen has always been associated with the concept of *Triturus* in its wide traditional acception, we decided to "validate" it for this subgenus, rather than coming a brand new nomen. In order to link both nomina "*Memus*" Rafinesque, 1815 and *Memus* nov. by an objective synonymy, we also hereby designate *Pelonectes boscai* Lataste in BLANCHARD, 1879: 276 as the nucleospecies of "*Memus*" Rafinesque, 1815 (**new nucleospecies designation**). This nomen will therefore now have to stand in the synonymy of *Memus* nov. (**new synonym**).

Several erroneous facts have been repeatedly copied in the literature regarding the nucleospecies of this subgenus. ASW mentions a nominal genus "*Pelonectes* Lataste in Tourneville, 1879", with the nucleospecies "*Pelonectes boscai* Lataste in Tourneville, 1879". If this was correct, this nomen "*Pelonectes* Lataste in Tourneville, 1879" would be a senior synonym of *Memus* nov., although invalid for being a junior homonym of *Pelonectes* Fitzinger, 1843 and *Pelonectes* Gistel, 1848.

MERTINS & WERMUTH (1960b: 25), THORN (1969: 248), FROST (1985: 614), MONTORI & HERRERO (2004: 233) and GARCÍA-PARIS et al. (2004: 593) also recognized a nominal species "*Pelonectes boscai* Lataste in Tourneville, 1879", but this is erroneous, for two distinct reasons. First, if the original description was indeed that published by TOURNEVILLE (1879), the author of the nomen would be "Tourneville", or "Lataste & Tourneville", because this paper clearly states that, whereas the original diagnosis that it reproduces had been written by Lataste, the complete description was written by Tourneville, at the request of Lataste himself (TOURNEVILLE, 1879: 69). However, this point is largely irrelevant, because the original description of the taxon had appeared earlier (BLANCHARD, 1879), in a work mentioned by TOURNEVILLE (1879: 71, footnote). This description appeared in the report of a meeting of the Société zoologique de France which makes it quite clear that both the new nomen and the Latin diagnosis of the new species were written, not by the secretary of the meeting, Raphael Blanchard, but by the author of the oral communication, Fernand Lataste. The latter alone is therefore the author of the new nomen *Pelonectes boscai*, according to Art. 50.2 of the Code.

A second mistake, present in ASW, in GORHAM (1974: 24) and in GARCÍA-PARIS et al. (2004: 593), is the recognition of a nominal genus "*Pelonectes* Lataste in Tourneville, 1879". There exists no such nominal taxon, not even as "*Pelonectes* Lataste in Blanchard, 1879". LATASTE (in BLANCHARD, 1879: 275) clearly stated that he was borrowing the nomen *Pelonectes* from FITZINGER (1843) as this nomen had "*remained without use*" ("*demouré sans emploi*"). The nucleospecies of *Pelonectes* FITZINGER, 1843: 33 is *Molge platycephala* Graenicher, 1829 by original designation, so that this generic nomen nowadays applies to the genus *Euproctus* Gene, 1839 which does not include the nominal species *Pelonectes boscai*, but this does not mean that Lataste created a new generic nomen: the erroneous allocation of a species to a genus does not result in the creation of a new junior homonymous nominal genus having this species as nucleospecies, because otherwise there would be dozens of thousands of such junior homonymous generic nomina in zootaxonomy!

As a consequence of this analysis, the generic nomen *Memus* nov. is the first one ever available for the genus including *Pelonectes boscai*.

Genus *Neuregerus* Cope, 1862

Comments A subjective synonym of the nomen of this genus is *Rhithrotriton* Nesterov, 1916. The site *ASW* states wrongly that its nucleospecies was never designated. In fact, this generic nomen was created for a taxon including two new nominal taxa: the species *Rhithrotriton derjugini* and the subspecies *Rhithrotriton derjugini microspilotus*. The latter taxon being of rank subspecies, and a single species being included in the taxon, *Rhithrotriton derjugini* is the nucleospecies of this genus by original monophory (**valid nucleospecies designation**) (see above for a general explanation of this situation)

Subgenus *Musergus* nov.

Nucleospecies. *Molge strauchii* Steindachner, 1888: 32, by present designation.

Etymology. From the Turkish *Mus* (name of the city which is the onymotope of the nucleospecies) and the final part (5 last letters) of the generic nomen *Neuregerus* Cope, 1862

Grammatical gender. - Masculine.

Entexognosis - The most inclusive holophyletic taxon including the species *Neuregerus strauchii* (Steindachner, 1888) and excluding the species *Neuregerus crocatus* (Cope, 1862)

Diagnosis. - See table 2

Idiognosis (1) TL up to 190 mm (2) Habitus stout. Body flattened. (3) Ventral coloration mainly dark, with median longitudinal orange band. (4) Sex dimorphism moderate. Coloration of side of tail in breeding male silver blue (5) Reproduction in lotic habitat (6) HAT (7) Northern eastern Turkey

Subgenus *Neuregerus* Cope, 1862

Nucleospecies *Neuregerus crocatus* Cope, 1862: 343, by original specific monophory

Etymology From the Greek *neuron* ("sinew, tendon") and *eigon* ("work")

Grammatical gender. - Masculine.

Entexognosis The most inclusive holophyletic taxon including the species *Neuregerus crocatus* (Cope, 1862) and excluding the species *Neuregerus strauchii* (Steindachner, 1888)

Diagnosis. See table 2

Idiognosis (1) TL 140-180 mm (2) Habitus stout. Body flattened (3) Ventral coloration bright (4) Sex dimorphism moderate. Coloration of side of tail in breeding not silver blue (5) Reproduction in lotic or lentic habitat (6) LAT or HAT (7) Southern eastern Turkey, western Iran and northern Irak

Genus *Triturus* Rafinesque, 1815Subgenus *Pyronicia* Gray, 1858

Nucleospecies *Salamandra marmorata* Latreille, 1800: 29, by present designation

Etymology. - Probably from the Greek *pur* ("fire") and *nikao* ("I prevail, I am victorious"), possibly meaning that in Europe salamanders have long been believed to cross fire and survive

Grammatical gender. - Feminine.

Entexognosis. - The most inclusive holophyletic taxon including the species *Triturus marmoratus* (Latreille, 1800) and excluding the species *Triturus cristatus* (Laurenti, 1768)

Diagnosis. - See table 2.

Idiognosis. (1) TL 100-180 mm (2) **Habitus** stout Head wide Skin very granular (3) **Dorsal coloration** green Ventral coloration black and white (4) **Sex dimorphism** strong. Dorsal crest of breeding male undulating. (5) **Highly terrestrial.** (6) **LAT.** (7) **Western Europe.**

Comments Until this work, no nomen was clearly available for this subgenus, but three genus-series nomina that can apply to this group were still awaiting a designation of nucleospecies, so that one of them can be resurrected for this purpose: *Hemmsalamandra* Duges, 1852, *Pyronicia* Gray, 1858, and *Neotriton* Bolckay, 1927 We chose the second of these three nomina because it is one of the shortest two (9 letters vs. respectively 14 and 9) and it sounds to us by far the most euphonious of the three. Besides, at least to a French reader, the nomen *Pyronicia* carries a message of beauty and "nobleness" that fully applies, in our opinion, to the majestic species *Triturus marmoratus* and its allies. Let us consider these three nomina successively.

The generic nomen *Hemmsalamandra* Duges, 1852: 254, 256 appears in *ASW* in the synonymies of both *Lissotriton* and *Triturus*. This nomen was created by DUGES (1852) with eleven originally included nominal species, two considered valid (*Salamandra marmorata* Latreille, 1800 and *Triton cristatus* Laurenti, 1768), and nine considered their synonyms (one of the former, eight of the latter), some of which are indeed now referred to the genus *Lissotriton*. Designating *Salamandra marmorata* as the nucleospecies of this genus would validate a nomen which is not only 14 letters long, but also misleading in suggesting that this genus belongs in the "true salamanders" rather than in the "newts". We therefore designate hereby *Triton cristatus* Laurenti, 1768: 39 as the nucleospecies of *Hemmsalamandra* Duges, 1852 (**new nucleospecies designation**). This nomen will therefore permanently stand in the synonymy of *Triturus* Rafinesque, 1815 as an objective synonym (**new synonym**).

The generic nomen *Pyronicia* Gray, 1858: 140 also appears in *ASW* in the synonymies of both *Lissotriton* and *Triturus*. It was created with four originally included nominal species, two considered valid (*Salamandra marmorata* Latreille, 1800) and *Salamandra punctata* Latreille, 1800), and two considered synonyms of the latter (the last three being now members of the hyponymous subgenus *Lissotriton*). We hereby designate *Salamandra marmorata* Latreille, 1800: 29 as the nucleospecies of *Pyronicia* Duges, 1858 (**new nucleospecies designation**), which consequently becomes the valid nomen for the subgenus including it and its close allies.

The nomen *Neotriton* Bolkay, 1927, 65 was created at subgeneric rank within *Triton* Laurenti, 1768, without nucleospecies designation, but with mention of at least four included taxa among at least six, as two of these taxa were given the rank subspecies and no other subspecies of the same species was cited. The four nominal species cited are *Triton blasii* De l'Isle du Dreneuf, 1862, *Triton cristatus* Laurenti, 1768, *Triton karelini* Strauch, 1870 and *Salamandra marmorata* Latreille, 1800. We hereby designate *Triton karelini* Strauch, 1870: 42 as nucleospecies of this nominal genus (**new nucleospecies designation**). This nomen will therefore now have to stand in the synonymy of the hyponymous subgenus *Triturus* Rafinesque, 1815 as a subjective synonym (**new synonym**).

Subgenus *Triturus* Rafinesque, 1815

Nucleospecies. – *Triton cristatus* Laurenti, 1768: 39, by subsequent designation of FITZINGER (1843: 34) under *Triton* Laurenti, 1768: 37.

Etymology. Apparently directly derived from the generic nomen *Triton* Laurenti, 1768: 37. The ending *-urus* reminds the Greek root *oura* ("tail") but is unlikely to be part of the etymology of *Triturus*, as the latter term would then mean "having a tail of *Triton*", i.e. 'having its own tail'.

Grammatical gender. – Masculine.

Entexognosis. – The most inclusive holophyletic taxon including the species *Triturus cristatus* (Laurenti, 1768) and excluding the species *Triturus marmoratus* (Latreille, 1800).

Diagnosis. – See table 2.

Idiognosis (1) TL 160-180 mm (2) Habitus slender. Head narrow. Skin granular. (3) Dorsal coloration black. Ventral coloration yellow or orange with black spots. (4) Sex dimorphism strong. Dorsal crest of breeding male denticulated. (5) Rather aquatic. (6) HAT. (7) Europe to Caucasus and Iran.

Comments As discussed above, the nomen *Triturus* Rafinesque, 1815 is a neonym for *Triton* Laurenti, 1768. The latter being preoccupied, *Triturus* is the valid nomen for the genus, having priority over the other three neonyms subsequently published for *Triton* Laurenti, 1768 (*Molge* Merrem, 1820; *Onacurus* Leuckart, 1821; *Tritonella* Swanson, 1839). Its nucleospecies is *Triton cristatus* Laurenti, 1768 by subsequent designation, under *Triton*, of FITZINGER (1843: 34). This nomen has several other synonyms, *Petraponia* Massalongo, 1853: 14 (nucleospecies, *Petraponia nigra* Massalongo, 1853: 15, by original specific monophory), *Turanomolge* Nikolsky, 1918: 182 (nucleospecies, by original specific monophory), *Turanomolge mensieri* Nikolsky, 1918: 182), *Alethotriton* Fatio, 1872: 517, and *Neotriton* Bolkay, 1927: 65. The nucleospecies of the latter two have not been properly identified so far, thus requiring a brief discussion.

Concerning the subgeneric nomen *Alethotriton* Fatio, 1872, ASH writes "Type species: *Triton cristatus* Laurenti, 1768, by implication". As reminded above, the *Code* does not recognize nucleospecies designations "by implication", so this information is incorrect. In fact, FATIO (1872: 516, 518) had twice expressly written that the nominal species

Triton cristatus Laurenti, 1768 was the "type" of this subgenus, thus making an original nucleospecies designation (**valid nucleospecies designation**). This nomen is therefore an invalid junior objective synonym of *Triturus Rafinesque*, 1815 (**new synonym**).

As for the nomen *Neotriton* Bolokay, 1927, it was discussed above under *Pyroniecia*.

Subtribus *TARICHA* nov

Nucleogenus. *Taricha* Gray, 1850: 5, 15, by present designation.

Entexognosis The most inclusive holophyletic taxon including the species *Taricha torosa* (Rathke, 1833) and excluding the species *Triturus cristatus* (Laurenti, 1768).

Diagnosis. - See table 2.

Idiognosis. - (1) TL 100-220 mm (2) Habitus stout (3) Dorsal and ventral colorations very contrasted. (4) Sex dimorphism strong. Dorsal crest absent. (5) Breeding habitat lentic or lotic. Type III amplexus. (6) HAT. (7) Nearctic.

Genus *Notophthalmus* Rafinesque, 1820

Subgenus *Notophthalmus* Rafinesque, 1820

Nucleospecies. - *Triturus miniatus* Rafinesque, 1820, 5, by original specific monophory.

Etymology From the Greek *notos* ("the back") and *ophthalmos* ("eye").

Grammatical gender. - Masculine.

Entexognosis The most inclusive holophyletic taxon including the species *Notophthalmus miniatus* Rafinesque, 1820 and excluding the species *Notophthalmus meridionalis* (Cope, 1880).

Diagnosis. See table 2.

Idiognosis (1) TL 90-140 mm (2) Habitus stout (3) Dorsal coloration light-olive green, sometimes with red spots or lines, ventral coloration orange to yellow, both with small black spots. (4) Sex dimorphism strong. Black horny ridges present on thighs of male. (5) Very aquatic, breeding in cold water (6) HAT (7) Eastern North America (8) Eft stage and neoteny present.

Subgenus *Rafinus* nov.

Nucleospecies *Diemictylus miniatus meridionalis* Cope 1880: 30, by present designation

Etymology From the patronym of the naturalist Constantin Samuel Rafinesque-Schmaltz, who was born in Constantinople (now Istanbul) in 1783 and died in Philadelphia after an extraordinary life which would be worth several novels and movies (RAFINESQUE, 1836; WARRIN, 2004), and who contributed to the discovery and naming of many species of amphibians, in particular urodelans, in Europe and North America.

Grammatical gender. – Masculine.

Entexognosis. The most inclusive holophyletic taxon including the species *Notophthalmus meridionalis* (Cope, 1880) and excluding the species *Notophthalmus mniatus* Rafinesque, 1820

Diagnosis – See table 2.

Idiognosis. (1) TL 100-110 mm. (2) Habitus stout (3) Dorsal coloration olive green, without red coloration; ventral coloration orange to yellow, both with large black spots. (4) Sex dimorphism moderate. No transverse black horny ridges on thighs of male. (5) Aquatic only during breeding period, in warm water (6) HAT (7) Texas and north-eastern Mexico (8) No eft stage, no neoteny.

Genus **Taricha** Gray, 1850

Subgenus **Taricha** Gray, 1850

Nucleospecies. *Triton torosa* Rathke, 1833 12, by original specific monophory

Etymology From the Greek *taikhos*, "mummy", probably because of the rough skin of these animals.

Grammatical gender. – Feminine

Entexognosis The most inclusive holophyletic taxon including the species *Taricha torosa* (Rathke, 1833) and excluding the species *Taricha rivularis* (Twitty, 1935).

Diagnosis. – See table 2.

Idiognosis (1) TL up to 220 mm (2) Habitus stout (3) Dorsal coloration brown, ventral coloration yellow-orange Iris yellow. (4) Sex dimorphism strong (5) Many eggs deposited in lentic habitat or few eggs deposited in lotic or lentic habitat (6) HAT (7) Western United States of America and western Canada

Subgenus **Twittyia** nov.

Nucleospecies *Triton rivularis* Twitty, 1935 73, by present designation.

Etymology From the patronym of Victor Chandler Twitty (1901-1967), who contributed to the knowledge of North American urodelans, in particular of the genus *Taricha*, and wrote the nice little book *Of scientists and salamanders* (TWITTY, 1966)

Grammatical gender. – Feminine

Entexognosis The most inclusive holophyletic taxon including the species *Taricha rivularis* (Twitty, 1935) and excluding the species *Taricha torosa* (Rathke, 1833)

Diagnosis. – See table 2.

Idiognosis (1) TL up to 190 mm (2) Habitus stout (3) Dorsal coloration black ventral coloration tomato red. Iris black (4) Sex dimorphism rather weak. (5) Few eggs deposited in lotic habitat. (6) HAT. (7) Western United States of America

Tribus *PLEURODELEINI* Tschudi, 1838

Nucleogenus. *Pleurodeles* Michahelles, 1830: 195, by implicit etymological designation

Entexognosis The most inclusive holophyletic taxon including the species *Triturus cristatus* (Laurenti, 1768) and excluding the species *Pleurodeles waltl* (Michahelles, 1830).

Diagnosis. – See table 2.

Genus *Tylotriton* Anderson, 1871Subgenus *Tylotriton* Anderson, 1871

Nucleospecies *Tylotriton verrucosus* Anderson, 1871: 423, by original specific monophory.

Etymology – From the Greek *tulos* ("swelling") and the generic nomen *Triton* Laurenti, 1768

Grammatical gender. – Masculine.

Entexognosis The most inclusive holophyletic taxon including the species *Tylotriton verrucosus* Anderson, 1871 and excluding the species *Tylotriton asperimus* (Unterstein, 1830)

Diagnosis See table 2

Idiognosis (1) TL 160-230 mm (2) Habitus stout. Cephalic ridges very developed. Vertebral ridge sharp. (3) Dorsal coloration usually rather bright, ventral coloration black to light (4) Sex dimorphism strong (5) Aquatic during breeding period. Eggs rather small, deposited in water (6) HAT (7) Bhutan, China, India, Laos, Myanmar, Nepal, Thailand

Subgenus *Yaotriton* nov

Nucleospecies *Tylotriton asperimus* Unterstein, 1830: 314, by present designation

Etymology – From the Chinese *Yao* (name of the mountain, the Yao Shan, which is the onymotope of the nucleospecies) and the generic nomen *Triton* Laurenti, 1768

Grammatical gender. – Masculine.

Entexognosis The most inclusive holophyletic taxon including the species *Tylotriton asperimus* (Unterstein, 1830) and excluding the species *Tylotriton verrucosus* Anderson, 1871

Diagnosis See table 2

Idiognosis (1) TL 170-190 mm (2) Habitus stout. Cephalic ridges very developed. Vertebral ridge very sharp. (3) Dorsal coloration black, ventral coloration black (4) Sex dimorphism weak (5) Terrestrial. Eggs large, deposited on land or in contact with water (6) IAT (7) Central and southern China, Vietnam.

Subfamilia *SALAMANDRINAE* Goldfuss, 1820

Nucleogenus *Salamandra* Laurenti, 1768: 41, by implicit etymological designation.

Entexognosis The most inclusive holophyletic taxon including the species *Salamandra salamandra* (Linnaeus, 1758) and excluding the species *Pleurodeles waltl* (Michahelles, 1830) and *Salamandrina perspicillata* (Savi, 1821).

Diagnosis. – See table 1.

Tribus *CHIOGLOSSINI* nov.

Nucleogenus – *Chioglossa* Bocage, 1864: 264, by present designation

Entexognosis The most inclusive holophyletic taxon including the species *Chioglossa lusitanica* Bocage, 1864 and excluding the species *Salamandra salamandra* (Linnaeus, 1758).

Diagnosis. – See table 2.

Idiognosis – (1) TL 150-200 mm. (2) Habitus slender. Tail very long. (3) Dorsal coloration dull with bright stripe or spots, ventral coloration dull. (4) Sex dimorphism strong, much longer tail in male. Forearm of breeding male enlarged. (5) Aquatic during breeding period. Eggs deposited in water. (6) LAT. (7) Western Iberian Peninsula, western Caucasus and north-eastern Turkey.

Tribus *SALAMANDRINI* Goldfuss, 1820

Nucleogenus. *Salamandra* Laurenti, 1768: 41, by implicit etymological designation

Entexognosis The most inclusive holophyletic taxon including the species *Salamandra salamandra* (Linnaeus, 1758) and excluding the species *Chioglossa lusitanica* Bocage, 1864.

Diagnosis – See table 2

Idiognosis (1) TL 110-320 mm. (2) Habitus stout. Tail short. (3) Dorsal coloration usually bright with spots or bands, ventral coloration dull. (4) Sex dimorphism moderate. Forearm of breeding male not enlarged. (5) Terrestrial, even during breeding period. Eggs deposited in water or retained in female (ovoviviparity or viviparity). (6) Usually HAT. (7) Western Palearctic.

Genus *Salamandra* Laurenti, 1768Subgenus *Algiandra* nov.

Nucleospecies *Salamandra maculosavar algina* Bedriaga, 1883: 252, by present designation

Etymology. – From the first four letters of the old German *Algierien* (“Algeria” name of the country including the only tope of the nucleospecies) and the last five letters of the generic nomen *Salamandra* Laurenti, 1768.

Table 4 Diagnostic comparisons among two groups composed of six parordinate taxa as recognized here

Superordinate taxon	Superspecies <i>Lissotriton (Lissotriton) vulgaris</i> (Linnaeus, 1758)					
Parordinate taxa	Species <i>Lissotriton graecus</i> (Wolterstorff, 1905)	Species <i>Lissotriton kostwae</i> (Freytag, 1955)	Species <i>Lissotriton lewisi</i> (Wolterstorff, 1914)	Species <i>Lissotriton meridionale</i> (Boulenger, 1882)	Species <i>Lissotriton monticola</i> (Boulenger, 1880)	Species <i>Lissotriton vulgaris</i> (Linnaeus, 1758)
Size of male	Small to large (TL 75-100 mm)	Small (TL 70-80 mm)	Large (TL 75-110 mm)	Small (TL 60-80 mm)	Large (TL 70-100 mm)	Large (TL 100-110 mm)
Habitus	Stout	Rather stout	Stout	Slender	Stout	Stout
Development of dorsal crest in breeding male	Low	Medium	High	Low	Low	High
Beginning of dorsal crest in breeding male	Back of head	Level of forelimbs	Back of head	Back of head	Back of head	Back of head
Shape of dorsal crest in breeding male	Straight	Straight	Undulating	Straight	Straight	Undulating
Dorsolateral ridge in breeding male	Present	Very sharp	Weak	Present	Very sharp	Absent
Palm or fringe on toes in breeding male	Moderate	Large	Large	Small	Absent	Very small
T ₂ fin in breeding male	Present (to 7 mm)	Present (to 9 mm)	Present (to 7 mm)	Present (to 8 mm)	Present (to 4 mm)	Absent
Size of rounded spots on male dorsum	Large	Large	Large	Small	Absent	Large or small
Colour of rounded spots on male venter	Blue-black	Blue-black	Black	Black	Absent	Black
Habitat	Mostly aquatic	Mostly aquatic	Mostly aquatic	Mostly aquatic	Mostly terrestrial	Mostly terrestrial
Adaptability in terrarium	HAT	LAT	HAT	LAT	LAT	HAT
Superordinate taxon	Genus <i>Salamandra</i> Laurenti, 1768					
Parordinate taxa	Subgenus <i>Alpandria</i> nov.	Subgenus <i>Alpandria</i> nov.	Subgenus <i>Corsandra</i> nov.	Subgenus <i>Mumandra</i> nov.	Subgenus <i>Orandrea</i> nov.	Subgenus <i>Salamandra</i> Laurenti, 1768
Size	Medium to large	Small	Large	Medium	Large	Small to large
Dorsolateral or lateral glands	Dorsolateral	Dorsolateral	Dorsolateral	Dorsolateral	Dorsolateral	Dorsolateral
Head	Narrow, small	Narrow, medium	Wide, large	Wide, medium	Wide, medium to large	Narrow to wide small to medium
Snout	Pointed	Rounded	Rounded	Pointed	Rounded to moderately pointed	Pointed to rounded
Dorsal coloration	With yellow or red colour	Black, grey, brown	With yellow or red colour	Black	With yellow or red colour	With yellow, orange or red colour
Reproduction mode	Oviviparity lecithotroph or viviparity adelphotroph	Viviparity matrotroph	Oviviparity lecithotroph	Viviparity matrotroph	Oviviparity lecithotroph	Oviviparity lecithotroph or viviparity adelphotroph
Adaptability in terrarium	LAT or HAT	LAT or HAT	HAT	LAT	Unknown	LAT or HAT

Grammatical gender. – Feminine.

Entoxognosis. The most inclusive holophyletic taxon including the species *Salamandra atra* Bedriaga, 1883 and excluding the species *Salamandra atra* Laurenti, 1768, *Salamandra atra* Savi, 1838, *Salamandra inframaculata* Martens, 1885, *Salamandra lunata* Nascetti, Andreone, Capula & Bullini, 1988 and *Salamandra salamandra* (Linnaeus, 1758).

Diagnosis. See table 4. See also table 2 for the diagnostic comparisons of the species *Salamandra atra* and *Salamandra atra*

Idiognosis. (1) TL up to 230 mm (2) Head narrow and small, snout pointed (3) Dorsolateral glands (4) Yellow spots, mainly regular, sometimes attenuated, sometimes red coloration on dorsal surfaces (5) Sex dimorphism moderate (6) Oviviparous lecithotroph or viviparous adelphotroph (7) Usually LAT, HAT in *Salamandra atra* (8) Northern Africa.

Subgenus **Alpandra** nov

Nucleospecies *Salamandra atra* Laurenti, 1768 42, by present designation

Etymology. From the Latin *Alpes* (name of the mountains including the onymotope of the nucleospecies) and the last five letters of the generic nomen *Salamandra* Laurenti, 1768

Grammatical gender. – Feminine

Entexognosis The most inclusive holophyletic taxon including the species *Salamandra atra* Laurenti, 1768 and excluding the species *Salamandra algira* (Bedriaga, 1883), *Salamandra corsica* Savi, 1838, *Salamandra inframaculata* Martens, 1885, *Salamandra lanzai* Nascetti, Andreone, Capula & Bullini, 1988 and *Salamandra salamandra* (Linnaeus, 1758).

Diagnosis. See table 4 See also table 2 for the diagnostic comparisons of the species *Salamandra atra* and *Salamandra aurorae*.

Idiognosis (1) TL 130 mm (2) Head narrow and medium, snout rounded Dorsolateral glands. (3) Black or yellow bands (4) Sex dimorphism moderate (5) Viviparous matrotroph (6) Usually LAT, HAT in *Salamandra aurorae*. (7) Alps

Subgenus **Corsandra** nov.

Nucleospecies *Salamandra corsica* Savi, 1838 208, by present designation

Etymology From the Latin *Corsica* (name of the island including the onymotope of the nucleospec.es) and the last five letters of the generic nomen *Salamandra* Laurenti, 1768

Grammatical gender. Feminine

Entexognosis The most inclusive holophyletic taxon including the species *Salamandra corsica* Savi, 1838 and excluding the species *Salamandra algira* (Bedriaga, 1883), *Salamandra atra* Laurenti, 1768, *Salamandra inframaculata* Martens, 1885, *Salamandra lanzai* Nascetti, Andreone, Capula & Bullini, 1988 and *Salamandra salamandra* (Linnaeus, 1758)

Diagnosis – See table 4

Idiognosis. (1) TL up to 250 mm (2) Head wide and large, snout rounded Dorsolateral glands. (3) Many yellow spots, irregular (4) Sex dimorphism moderate (5) Oviviparous lecithotroph. (6) HAT. (7) Corsica

Subgenus **Mimandra** nov

Nucleospecies *Salamandra lanzai* Nascetti, Andreone, Capula & Bullini, 1988: 619, by present designation

Etymology From the Latin *mima* ("actress, female name") and the last five letters of the generic nomen *Salamandra* Laurenti, 1768 This nomen points to the fact that the nucleospecies of this subgenus was long confounded with the species *Salamandra atra* Laurenti, 1768, which is similar to it by its coloration, its reproductive mode (viviparity) and its Alpine distribution, before being discovered to resemble it by convergence.

Grammatical gender – Feminine.

Entoxognosis. – The most inclusive holophyletic taxon including the species *Salamandra lanzai* Nascetti, Andreone, Capula & Bullini, 1988 and excluding the species *Salamandra atra* (Bedriaga, 1883), *Salamandra atra* Laurenti, 1768, *Salamandra inframaculata* Martens, 1885, *Salamandra corsica* Savi, 1838 and *Salamandra salamandra* (Linnaeus, 1758)

Diagnosis. – See table 4.

Idiognosis (1) TL 160 mm (2) Head wide and medium, snout pointed. Lateral glands. (3) Black. (4) Sex dimorphism moderate. (5) Viviparous matrotroph (6) LAT. (7) South-western Alps.

Subgenus *Oriandra* nov.

Nucleospecies *Salamandra maculosa* var. *inframaculata* Martens, 1885, 195, by present designation.

Etymology. – From the first three letters of Latin *oriens* ("the East") and the last five letters of the generic nomen *Salamandra* Laurenti, 1768.

Grammatical gender. – Feminine.

Entoxognosis – The most inclusive holophyletic taxon including the species *Salamandra inframaculata* Martens, 1885 and excluding the species *Salamandra atra* (Bedriaga, 1883), *Salamandra atra* Laurenti, 1768, *Salamandra corsica* Savi, 1838, *Salamandra lanzai* Nascetti, Andreone, Capula & Bullini, 1988 and *Salamandra salamandra* (Linnaeus, 1758)

Diagnosis – See table 4

Idiognosis (1) TL up to 324 mm (2) Head wide, medium to large, snout rounded to moderately pointed. Dorsolateral glands (3) Many yellow spots, regular or irregular, very large or very small. (4) Sex dimorphism moderate (5) Oviparous lecithotroph (6) Adaptability in captivity unknown (7) From Israel to western Iran

Subgenus *Salamandra* Laurenti, 1768

Nucleospecies *Salamandra maculosa* Laurenti, 1768–42, by subsequent designation of FITZINGER, 1843, 33

Etymology – From the Latin *salamandra* ("salamander")

Grammatical gender. – Feminine.

Entoxognosis – The most inclusive holophyletic taxon including the species *Salamandra salamandra* (Linnaeus, 1758) and excluding the species *Salamandra atra* (Bedriaga, 1883), *Salamandra atra* Laurenti, 1768, *Salamandra corsica* Savi, 1838, *Salamandra inframaculata* Martens, 1885 and *Salamandra lanzai* Nascetti, Andreone, Capula & Bullini, 1988.

Diagnosis – See table 4. See also table I for the diagnostic comparisons of the species *Salamandra atra*, *Salamandra atra*, *Salamandra longirostris* and *Salamandra salamandra* and of the verges *crespoi*, *fastuosa* and *salamandra* of the latter species.

Idiognosis (1) TL 111-280 mm. (2) Head narrow to wide, small to medium, snout pointed to rounded Dorsolateral glands. (3) Spots or bands, yellow or sometimes orange (4) Sex dimorphism moderate (5) Ovoviviparous lecithotroph or viviparous adelphotroph. (6) LAT or HAT. (7) Southern and central Europe.

Comments. Following STEJNEGER (1936: 135), FROST (1985: 613) stated erroneously that the nucleospecies of this nominal genus was "*Salamandra maculosa* Laurenti, 1768 (= *Lacerta salamandra* Linnaeus, 1758) by tautonymy" MONTORI & HERRERO (2004: 55) also considered *Lacerta salamandra* Linnaeus, 1758 as the nucleospecies of this genus. However, as pointed out by DU BOIS (1987c: 136-137), this is impossible, as the nominal species *Lacerta salamandra* Linnaeus, 1758 was not part of the nominal species originally included in the genus. Nucleospecies of nominal genera are nominal species, not taxonomic species, and the synonymy between both nomina *Salamandra maculosa* Laurenti, 1768 and *Lacerta salamandra* Linnaeus, 1758 is subjective, even if widely accepted for two centuries, therefore liable to change. The valid designation of *Salamandra maculosa* Laurenti, 1768 as nucleospecies of this genus was made by FITZINGER (1843: 33) (**valid nucleospecies designation**).

A nomen which should stand in the synonymy of this genus is "*Salamandra*" Gronovius, 1763: 12 (**new synonym**). This is an anoplonym, as having been published in a work not using a binominal nomenclature for species (ANONYMOUS, 1925). In order to stabilize the place of this nomen in synonymies, we hereby designate *Salamandra maculosa* Laurenti, 1768 as its nucleospecies (**new nucleospecies designation**).

Subfamilia SALAMANDRININAE Fitzinger, 1843

Nucleogenus. - *Salamandrina* Fitzinger, 1826: 41, by implicit etymological designation

Entexognosis The most inclusive holophyletic taxon including the species *Salamandrina perspicillata* (Savi, 1821) and excluding the species *Pleurodeles waltl* (Michahelles, 1830) and *Salamandra salamandra* (Linnaeus, 1758)

Diagnosis. - See table I.

CONCLUSION

The ergotaxonomy of the family SALAMANDRIDAE here proposed (table 5) recognizes 253 taxa at 11 different ranks, including 118 species and 60 subspecies, grouped in 31 genera and 23 subgenera. From family to subspecies, the increase in the number of taxa at the four major ranks (family, genus, species and subspecies) is regular, as shown in fig. 2. This suggests that this ergotaxonomy is rather well balanced, at least as measured by the quantitative "metataxonomic criterion" described by VAN VALLIN (1973) and DU BOIS (1988a-b), but of course by itself this information does not mean that this taxonomy is "valid" by any other criterion.

Table 5 A complete ergotaxonomy of the family *Stammatridae* Goldfuss, 1820. Nomenclature of the family-series are printed in CAPITAL ITALIC and those of the genus- and species-series in italics. Abbreviations for ranks: sF, subfamily, T, tribus, sT, subtribus, iT, infratribus, G, genus, sG, subgenus; SS, supraspecies; S, species; E, exerge; sS, subspecies.

- sF T sT iT G sG SS S E sS
- PLFURODELINAE** Tschudi, 1838
- MOLGINI** Gray, 1850
- MOLGINA** Gray, 1850
- CYNOPITA** nov.
- † *Carpathotriton* Venzel, 2008
- † *Carpathotriton austriensis* Venzel, 2008
- Cynops* Tschudi, 1838
- Cynops ensicauda* (Hallowell, 1860)
- Cynops ensicauda ensicauda* (Hallowell, 1860)
- Cynops ensicauda popei* (Inger, 1947)
- Cynops pyrhogaster* (Boie, 1826)
- Hypselotriton** Walterstorff, 1934
- Hypselotriton* Walterstorff, 1934
- Hypselotriton (Hypselotriton) cheungangensis* (Kou & Xing, 1983)
- Hypselotriton (Hypselotriton) cyanurus* (Liu, Hu & Yang, 1962)
- Hypselotriton (Hypselotriton) cyanurus cyanurus* (Liu, Hu & Yang, 1962)
- Hypselotriton (Hypselotriton) cyanurus yunnanensis* (Yang, 1983)
- Hypselotriton (Hypselotriton) walterstorffi* (Boulenger, 1905)
- Pingia** Chang, 1935
- Hypselotriton (Pingia) grandosus* (Chang, 1933)
- Hypselotriton (Pingia) orientalis* (David, 1875)
- Hypselotriton (Pingia) orphicus* (Rösch, 1983)
- Lacotriton** nov.
- Lacotriton laosensis* (Stuart & Papenfuss, 2002)
- Pachytriton** Boulenger, 1878
- Pachytriton arc. hispidus* Shen, Shen & Mo, 2008
- Pachytriton brevipes* (Sausage, 1876)
- Pachytriton labiatus* (Untersiem, 1930)
- Paramesotriton** Chang, 1935
- Allomesotriton* Freytag, 1983
- Paramesotriton (Allomesotriton) cundapanitatus* (Liu & Hu in HU, DIAO & LIU, 1973)
- Paramesotriton* Chang, 1935
- Paramesotriton (Paramesotriton) chinensis* (Gray, 1859)
- Paramesotriton (Paramesotriton) dehoustali* (Bourret, 1934)
- Paramesotriton (Paramesotriton) fuchongensis* Wen, 1989
- Paramesotriton (Paramesotriton) guangxiensis* (Huang, Tang & Tang, 1983)
- Paramesotriton (Paramesotriton) longkengensis* (Myers & Leviton, 1962)
- Paramesotriton (Paramesotriton) longhensis* Li, Tian, Gu & Xiong, 2008
- Paramesotriton (Paramesotriton) zhijunensis* Li, Tian & Gu, 2008
- † *Procyrops* Young, 1965
- † *Procyrops mitchellii* Young, 1965
- EL PROXIMITA** nov.
- Euproctus** Cuvé, 1838
- Euproctus montanus* (Savi, 1838)
- Euproctus platycephalus* (Gravenhorst, 1829)
- MOLGITA** Gray, 1850
- Incertae sedis
- † *Iriturus lacustris* Lartet, 1851
- † *Iriturus minimus* Gröbel, 1847
- † *Iriturus subvannensis* Lartet, 1851
- † *Iriturus watershoffi* Linnaeu, 1950

Table 5. – (continued 1).

sF T sT iT G sG SS S E sS

- Calotriton* Gray, 1858
Calotriton arnoldi Carranza & Amat, 2005
Calotriton asper (Duges, 1852)
- Ichthyosaura* Sonnini & Latreille, 1801
Ichthyosaura alpestris (Laurenti, 1768)
alpestris (Laurenti, 1768)
Ichthyosaura alpestris (alpestris) alpestris (Laurenti, 1768)
Ichthyosaura alpestris (alpestris) apuana (Bonaparte, 1839)
Ichthyosaura alpestris (alpestris) cyreni (Wolterstorff, 1932)
Ichthyosaura alpestris (alpestris) inexpectata (Dubois & Breuil, 1983)
reiseri (Werner, 1902)
Ichthyosaura alpestris (reiseri) carpathica (Dely, 1959)
Ichthyosaura alpestris (reiseri) montenegrina (Radovanović, 1951)
Ichthyosaura alpestris (reiseri) reiseri (Werner, 1902)
Ichthyosaura alpestris (reiseri) veluchensis (Wolterstorff, 1935)
- † *Koallia* Herre, 1950
† *Koallia genzei* Herre, 1950
- Lissotriton* Bell, 1839
insertae sedis
† *Lissotriton opalinus* (Meyer, 1851)
† *Lissotriton rohrsi* (Herre, 1955)
- Lissotriton* Bell, 1839
helveticus (Razoumowsky, 1789)
Lissotriton (Lissotriton) (helveticus) helveticus (Razoumowsky, 1789)
Lissotriton (Lissotriton) (helveticus) helveticus almonii (Seoane, 1884)
Lissotriton (Lissotriton) (helveticus) helveticus helveticus (Razoumowsky, 1789)
Lissotriton (Lissotriton) (helveticus) helveticus punctillans (Schmidler, 1970)
- italicus* (Peracca, 1898)
Lissotriton (Lissotriton) (italicus) italicus (Peracca, 1898)
Lissotriton (Lissotriton) (italicus) italicus italicus (Peracca, 1898)
Lissotriton (Lissotriton) (italicus) italicus molisianus (Alibello, 1926)
- vulgaris* (Linnaeus, 1758)
Lissotriton (Lissotriton) (vulgaris) graecus (Wolterstorff, 1905)
Lissotriton (Lissotriton) (vulgaris) koxwigeri (Reytag, 1955)
Lissotriton (Lissotriton) (vulgaris) kurtzi (Wolterstorff, 1914)
Lissotriton (Lissotriton) (vulgaris) meridionalis (Boulenger, 1882)
Lissotriton (Lissotriton) (vulgaris) montandoni (Boulenger, 1880)
Lissotriton (Lissotriton) (vulgaris) vulgaris (Linnaeus, 1758)
Lissotriton (Lissotriton) (vulgaris) vulgaris ampelensis (Fuhn, 1951)
Lissotriton (Lissotriton) (vulgaris) vulgaris vulgaris (Linnaeus, 1758)
- Meinus* nov.
Lissotriton (Meinus) boscai (Lataste in Blanchard, 1879)
Lissotriton (Meinus) multzani (Boettger, 1879)
- Neurergus* Cope, 1862
Musergus nov.
- *Neurergus (Musergus) stranchii* (Steindachner, 1888)
Neurergus (Musergus) stranchii barani Oz, 1994
† *Neurergus (Musergus) stranchii stranchii* (Steindachner, 1888)
- Neurergus* Cope, 1862
Neurergus (Neurergus) crocatus Cope, 1862
Neurergus (Neurergus) kaiseri Schmidt, 1952
Neurergus (Neurergus) microspilotus (Nesterov, 1916)
- † *Oligosemia* Navas, 1922
† *Oligosemia spinosa* Navas, 1922

Table 5. – (continued 2)

sF T sT IT G sG SS S E sS

Ommatotriton Gray, 1850*Ommatotriton ophryticus* (Berthold, 1846)*Ommatotriton ophryticus nesterovi* Litvinchuk, Zuiderwijk, Borkin & Rosanov, 2005*Ommatotriton ophryticus ophryticus* (Berthold, 1846)*Ommatotriton vittatus* (Gray, 1835)*Ommatotriton vittatus cilicicus* (Wolterstorff, 1906)*Ommatotriton vittatus vittatus* (Gray, 1835)*Triturus* Rafinesque, 1815*Pyronota* Gray, 1858*Triturus (Pyronota) marmoratus* (Latreille, 1800)*Triturus (Pyronota) pygmaeus* (Wolterstorff, 1905)*Triturus* Rafinesque, 1815*Triturus (Triturus) cornifex* (Laurenti, 1768)*Triturus (Triturus) cristatus* (Laurenti, 1768)*Triturus (Triturus) dobrogeicus* (Kiritzescu, 1903)*Triturus (Triturus) dobrogeicus dobrogeicus* (Kiritzescu, 1903)*Triturus (Triturus) dobrogeicus macrosoma* (Boulenger, 1908)*Triturus (Triturus) karelini* (Strauch, 1870)*Triturus (Triturus) karelini arizemii* Litvinchuk, Borkin, Druzic & Kateric, 1999*Triturus (Triturus) karelini karelini* (Strauch, 1870)*Triturus (Triturus) macedonicus* (Karaman, 1922)**TARICHTINA** nov.*Notophthalmus* Rafinesque, 1820

Incertae sedis

† *Notophthalmus crassus* Tihen, 1974† *Notophthalmus rubrivus* Estes, 1963*Notophthalmus* Rafinesque, 1820*Notophthalmus (Notophthalmus) persaratus* (Bishop, 1941)*Notophthalmus (Notophthalmus) viridescens* (Rafinesque, 1820)*Notophthalmus (Notophthalmus) viridescens dorsalis* (Harlan, 1828)*Notophthalmus (Notophthalmus) viridescens louisianensis* Wolterstorff, 1914*Notophthalmus (Notophthalmus) viridescens parvirostris* (Schwartz & Duellman, 1952)*Notophthalmus (Notophthalmus) viridescens viridescens* (Rafinesque, 1820)*Rafinus* nov.*Notophthalmus (Rafinus) meridionalis* (Cope, 1880)*Notophthalmus (Rafinus) meridionalis kallerii* (Wolterstorff, 1930)*Notophthalmus (Rafinus) meridionalis meridionalis* (Cope, 1880)*Taricha* Gray, 1850

Incertae sedis

† *Taricha hindsii* Bevier, 1979† *Taricha mionemica* Tihen, 1974† *Taricha oligoneura* (Van Frank, 1955)*Taricha* Gray, 1850*Taricha (Taricha) granulosa* (Skilton, 1849)*Taricha (Taricha) haasi stewarti* (Twitty, 1942)*Taricha (Taricha) haasi torosa* (Rathke, 1833)*Twittia* nov.*Taricha (Twittia) eximius* (Twitty, 1935)**PTEUROHELINI** Tschudi, 1838

Incertae sedis

† *Tetanus s. hynithi* (Herc & Linné, 1756)† *Brachycornus* Meyer, 1860† *Brachycornus novae havis* (Goldfuss, 1831)† *Chelotriton* Pomel, 1853† *Chelotriton oxygus* (Goldfuss, 1831)† *Chelotriton paradoxus* Pomel, 1853† *Chelotriton pluvencus* Bailon, 1989† *Chelotriton robustus* Westphal, 1979

Table 5. – (continued 3).

sf T sT iT G sG SS S E sS

- Echinotriton* Nussbaum & Brodie, 1982
Echinotriton andersoni (Boulenger, 1892)
Echinotriton chulabunensis (Chang, 1932)
 † *Palaevopleurodeles* Herre, 1941
 † *Palaevopleurodeles bouffi* Herre, 1941
Pleurodeles Michahelles, 1830
Pleurodeles nebulosus (Guichenot, 1850)
Pleurodeles pourti (Geayss, 1835)
Pleurodeles waltl Michahelles, 1830
Tylosotriton Anderson, 1871
 Incertae sedis
 † *Tylosotriton weigelti* Herre, 1935
Tylosotriton Anderson, 1871
Tylosotriton (*Tylosotriton*) *kwetchowensis* Fang & Chang, 1932
Tylosotriton (*Tylosotriton*) *shungui* Nussbaum, Brodie & Yang, 1995
Tylosotriton (*Tylosotriton*) *taihangensis* Liu, 1950
Tylosotriton (*Tylosotriton*) *verrucosus* Anderson, 1871
Yaotriton nov.
Yaotriton (*Yaotriton*) *asperimus* Unterstein, 1930
Yaotriton (*Yaotriton*) *hamanensis* Fei, Ye & Yang, 1984
Yaotriton (*Yaotriton*) *vietnamensis* Bohme, Schönle, Nguyen & Köhler, 2005
Yaotriton (*Yaotriton*) *wenxiensis* (Fei, Ye & Yang, 1984)

SALAMANDRINAE Goldfuss, 1820

CIBIOLASSINI nov

- Cibiolassa* Bocage, 1864
Cibiolassa lusitanica Bocage, 1864
Cibiolassa lusitanica longipes Arnzen, Groenenberg, Alexandrino, Ferrand & Scyres, 2007
Cibiolassa lusitanica lusitanica Bocage, 1864
 † *Cibiolassa microtiles* & Hoffstetter, 1976
Mertensiella Wolfenstorf, 1975
Mertensiella ambigua (Waga, 1876)
 † *Mertensiella mera* Hedrova, 1984

SALAMANDRINI Goldfuss, 1820

- Lyciasalamandra* Veith & Steinfartz, 2004
Lyciasalamandra antalyana (Basoglu & Baran, 1976)
Lyciasalamandra atifi (Basoglu, 1967)
Lyciasalamandra bilbae (Franzen & Klwen, 1987)
Lyciasalamandra fatizae (Basoglu & Atatur, 1974)
Lyciasalamandra flavimembra (Mutz & Steinfartz, 1995)
Lyciasalamandra helverseni (Pieper, 1963)
Lyciasalamandra loschani (Stenbacher, 1891)
Lyciasalamandra loschani bersoglu (Baran & Atatur, 1980)
Lyciasalamandra loschani flinkensis (Basoglu & Atatur, 1975)
Lyciasalamandra loschani loschani (Stenbacher, 1891)
 † *Megalotriton* Zittel, 1890
 † *Megalotriton fallboldi* Zittel, 1890
Salamandra Laurent, 1768
 Incertae sedis
 † *Salamandra gausserihami* Lartet, 1851
 † *Salamandra samsanensis* Lartet, 1851
Ulyandora nov.
Salamandra (*Algyndora*) *algira* Bedriaga, 1883
Salamandra (*Algyndora*) *algira algira* Bedriaga, 1883
Salamandra (*Algyndora*) *algira splucua* Iscoriza & Couas, 2007
Salamandra (*Algyndora*) *trichota* (Doron, Battoso & Bogart, 2003)

Table 5. - (continued 4).

sF	T	sT	IT	G	sG	SS	SS	E	sS
									<i>Alpandra</i> nov.
									<i>Salamandra</i> (<i>Alpandra</i>) <i>atra</i> Laurenti, 1768
									<i>Salamandra</i> (<i>Alpandra</i>) <i>atra atra</i> Laurenti, 1768
									<i>Salamandra</i> (<i>Alpandra</i>) <i>atra pasubensis</i> Bonato & Steinfartz, 2005
									<i>Salamandra</i> (<i>Alpandra</i>) <i>atra prenjensis</i> Miksic, 1969
									<i>Salamandra</i> (<i>Alpandra</i>) <i>aurorae</i> Trevisan, 1982
									<i>Corsandra</i> nov.
									<i>Salamandra</i> (<i>Corsandra</i>) <i>corstra</i> Savi, 1838
									<i>Mimandra</i> nov.
									<i>Salamandra</i> (<i>Mimandra</i>) <i>lanzae</i> Nascetti, Andreone, Capula & Bullini, 1988
									<i>Orandria</i> nov.
									<i>Salamandra</i> (<i>Orandria</i>) <i>infraannulata</i> Martins, 1885
									<i>Salamandra</i> (<i>Orandria</i>) <i>infraannulata infraannulata</i> Martins, 1885
									<i>Salamandra</i> (<i>Orandria</i>) <i>infraannulata orientalis</i> Wolterstorff, 1925
									<i>Salamandra</i> (<i>Orandria</i>) <i>infraannulata senevovi</i> Nestler, 1916
									<i>Salamandra</i> Laurenti, 1768
									<i>Salamandra</i> (<i>Salamandra</i>) <i>atimanzonis</i> Muller & Hellmich, 1935
									<i>Salamandra</i> (<i>Salamandra</i>) <i>longirostris</i> Joger & Steinfartz, 1994
									<i>Salamandra</i> (<i>Salamandra</i>) <i>salamandra</i> (Linnaeus, 1758)
									<i>crespus</i> Malkmus, 1983
									<i>Salamandra</i> (<i>Salamandra</i>) <i>salamandra</i> (<i>crespus</i>) <i>crespus</i> Malkmus, 1983
									<i>Salamandra</i> (<i>Salamandra</i>) <i>salamandra</i> (<i>crespus</i>) <i>morenica</i> Joger & Steinfartz, 1994
									<i>fastuosa</i> Schreiber, 1912
									<i>Salamandra</i> (<i>Salamandra</i>) <i>salamandra</i> (<i>fastuosa</i>) <i>alfredschmidti</i> Köhler & Steinfartz, 2006
									<i>Salamandra</i> (<i>Salamandra</i>) <i>salamandra</i> (<i>fastuosa</i>) <i>bernardini</i> Wolterstorff, 1928
									<i>Salamandra</i> (<i>Salamandra</i>) <i>salamandra</i> (<i>fastuosa</i>) <i>fastuosa</i> Schreiber, 1912
									<i>Salamandra</i> (<i>Salamandra</i>) <i>salamandra</i> (<i>fastuosa</i>) <i>gleditsi</i> I selt & Lanza, 1956
									<i>salamandra</i> (Linnaeus, 1758)
									<i>Salamandra</i> (<i>Salamandra</i>) <i>salamandra</i> (<i>salamandra</i>) <i>berguae</i> Wolterstorff, 1934
									<i>Salamandra</i> (<i>Salamandra</i>) <i>salamandra</i> (<i>salamandra</i>) <i>berghavi</i> Obst, 1981
									<i>Salamandra</i> (<i>Salamandra</i>) <i>salamandra</i> (<i>salamandra</i>) <i>galliae</i> Seign, 1885
									<i>Salamandra</i> (<i>Salamandra</i>) <i>salamandra</i> (<i>salamandra</i>) <i>salamandra</i> (Linnaeus, 1758)
									<i>Salamandra</i> (<i>Salamandra</i>) <i>salamandra</i> (<i>salamandra</i>) <i>terrestris</i> Bonnatere, 1789
									<i>Salamandra</i> (<i>Salamandra</i>) <i>salamandra</i> (<i>salamandra</i>) <i>verneri</i> Sochurek & Cayda, 1941
									SALAMANDRINAE Fitzinger, 1843
									† <i>Archaeostrotion</i> Mever, 1860
									† <i>Archaeostrotion bisulcatus</i> (Meyer, 1860)
									<i>Salamandrina</i> Fitzinger, 1826
									<i>Salamandrina</i> <i>perspicillata</i> (Savi, 1821)
									<i>Salamandrina</i> <i>terdigitata</i> (Bonnaterre, 1789)

The ergotaxonomy here presented includes 253 situations of hypotaxy as defined above (see table 6), which are distributed as follows in the four categories distinguished above: (1) 52 cases (20.6%) of monohypotaxy, (2) 25 cases (9.9%) of dihypotaxy, (3) 17 cases (6.7%) of polyhypotaxy, and (4) 159 cases (62.8%) of anhypotaxy, including 99 species without subspecies and 60 subspecies. In this case, as we used a finely divided nomenclatural hierarchy to express this taxonomy, all cases of polyhypotaxy can be considered to express unresolved polytomies. As they amount for less than 7% of cases, this suggests that for this family of salamanders the available data support rather well resolved relationships between taxa. This does not mean at all that this ergotaxonomy is "final", especially as new taxa certainly await discovery and description.

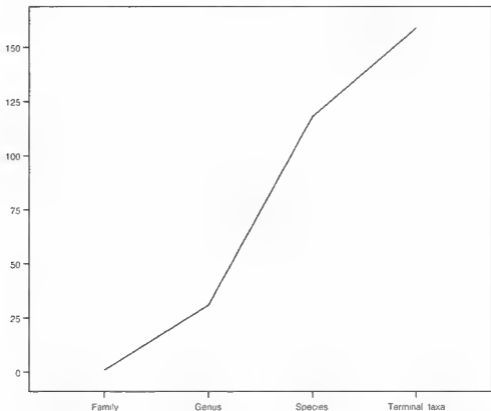


Fig. 2. Number of taxa at the four major ranks (family, genus, species and "terminal taxon" (i.e., either species or subspecies)) recognized in the ergotaxonomy of the *SUAMENIDRIDE* here adopted.

To express this rather detailed hierarchical ergotaxonomy, less nomina than taxa are necessary, as expressed by the nomenclatural parsimony ratio defined above. In the family-series, only 8 nomina (including 4 new ones, i.e., 50.0%) are needed for 13 taxa (NPR 61.5%). In the genus-series, 44 nomina (including 11 new ones, i.e., 25.0%) are needed for 54 taxa (NPR 81.5%). In the species-series, 148 nomina (without any new one) are needed for 186 taxa (NPR 79.0%).

The 11 genus-series nomina created here have from 6 to 9 letters (mean 8.0, median 8.0). This results in a decrease in the mean (10.3 vs. 11.6) and median (10.0 vs. 11.0) numbers of letters of the generic nomina of the whole family (see above), which however is not significant, although almost so, compared to the previous situation (Mann-Whitney U -test, $U = 628.5$, $P = 0.052$). This number remains significantly higher than in the *REVIBU* (Mann-Whitney U -test, $U = 497.5$, $P = 0.002$). This is because very long nomina created previously in the *SUAMENIDRIDE* still remain (and will have to remain) in use in this family. However, a strong change in the historical trend in the length of nomina over time since 1758 is now evident.

Table 6 – Number of cases of each category of hypotaxy (see text for explanation) represented at each rank in the ergotaxonomy of the *SALAMANDRIDAE* here proposed. Ranks: F, familia, sF, subfamilia, T, tribus, sT, subtribus, iT, infratribus, G, genus, sG, subgenus; SS, supraspecies, S, species, E, exerge; sS, subspecies.

Category of hypotaxy	F	sF	T	sT	iT	G	sG	SS	S	E	sS	Total
Monoypotaxy	0	1	3	1	1	22	22	2	0	0	0	52
Diploypotaxy	0	2	1	0	0	8	0	0	13	1	0	25
Polyhypotaxy	1	0	0	1	2	1	1	1	6	4	0	17
Anhypotaxy	0	0	0	0	0	0	0	0	99	0	60	159
Total	1	3	4	2	3	31	23	3	118	5	60	253

(fig. 1). We suggest a similar voluntary limitation in the length and complexity of generic nomina would be beneficial in all other amphibian families, and probably also over the whole of zootaxonomy. Non-taxonomists are looking at taxonomists and their works, and they often make negative comments on the "barbarian" nomina often given to taxa by the latter.

As mentioned above, the taxonomic impediment is still quite important in almost all groups of amphibians. Although long studied, the taxonomy of the salamanders of the family *SALAMANDRIDAE* is still not stabilized and should not be considered so. In the future years and decades, we will certainly witness many descriptions of new species, subspecies and taxa at various levels above species, changes of ranks for already recognized taxa (e.g., subspecies elevated to species rank) and "resurrection" of once synonymized nomina. We think that this trend will allow a better protection and conservation of these endangered organisms. At the beginning of the century of extinctions (DUBOIS, 2003a), the role of taxonomy is an important one. As we have seen, legislative texts that have consequences on the conservation of amphibian populations or habitats are highly dependent on the existence of formally named taxa, which can be placed on "official lists". Therefore, as soon as they have data, even preliminary, pointing to the distinctness or uniqueness of populations or groups, taxonomists should seriously consider recognizing the latter as formal taxa and naming them. Refraining too long from recognizing new taxa because of "uncertainties" is not doing a service to the study and conservation of biodiversity. It is better to have to synonymize a nomen when new data suggest that the taxon for which it was coined was unwarranted than being unable to protect an interesting or unique population because it does not bear a special nomen. We live at a special period of the history of taxonomy when "taxonomic cramps" amount to genuine errors.

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